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**COMPARATIVE STUDIES ON THE MORPHOLOGY OF MALE
SCALE INSECTS (HEMIPTERA: COCCOIDEA)***

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J. G. THERON, M.Sc., Ph.D.

(Dept. of Entomology, University of Stellenbosch)

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ABSTRACT

In the present work the external morphology of 7 species of male coccids, namely *Margarodes vitium*, *Pseudaspidoproctus* (?)fullery, *Steingelia gorodetskia*, *Eulecanium taxi*, *Pseudococcus citri*, *Aulacaspis pentagona* and *Diaspidiotus bavaricus*, is studied in detail. Male coccids are very specialized when compared with other Sternorrhyncha, mainly because of the lack of functional mouth parts, the reduction of the hind wings to halteres and the desclerotization of the body wall. It was found that *Margarodes* is the most primitive of the species studied and it is probably more closely related to the Aphidoidea than to any of the other Sternorrhynchan groups. In *Margarodes* and *Pseudaspidoproctus* the large compound eyes have been replaced by simple eyes. Larval eyes also persist in the adults, except in *Aulacaspis* and *Diaspidiotus* where they are degenerate. Because of desclerotization the head is reinforced by secondary preocular, postocular and preoral ridges. The thorax is more typical of the general homopteran thorax than the head is of the homopteran head, but the mesopostnotum has two postnotal apophyses and the metathorax is very much reduced. The abdomen is largely desclerotized and the genitalia are relatively simple as no periphallallic structures are present; the genitalia consist only of a penis and penial sheath, which may be elongate.

* Most of the information contained in this paper was submitted in the form of a thesis for the degree of Ph.D. of the University of London, Oct., 1955.

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I. INTRODUCTION

Although a vast amount of work has already been done on the anatomy and classification of female coccids, the morphology of the male has, with very few exceptions, been largely neglected and the present study has been undertaken in an attempt to remedy this. There are various reasons for the lack of information on the structure of male coccids. An important factor is that in many species the male is relatively rare and appears seasonally, or is apparently completely absent. Furthermore, as male coccids are short-lived and very small, the adults are rarely encountered in the field and therefore have to be bred out in the laboratory. In addition to their being diminutive, most of them are also very delicate and a detailed study of their morphology presents many technical difficulties.

A better understanding of the anatomy of male coccids is however essential, since, as Ferris (1942, 1950) points out, no satisfactory system of classification can be achieved before more is known about the structure of the males. Up to now the classification of coccids has been based almost exclusively on the structural characters of the female, but since the females are neotenic (Reh, 1901; Börner, 1910) it is very difficult to arrive at a natural classification by utilizing only the specialized characters which they afford. The neotenic nature of the female, which is an atypical specialized Sternorrhynchan feature, also means that the affinities of the Coccoidea with other Sternorrhyncha can only be decided from males. According to both Balachowsky (1937) and Ferris (1937) the structure of the males may be of great importance in determining the relationships of the higher categories of the group, but is relatively unimportant in distinguishing between species. A thorough investigation might well prove, however, that the taxonomic characters of the male are just as important on the specific level.

Most of the available information on male coccids is found in papers dealing primarily with taxonomy and consists mainly of brief notes on the more obvious features of their anatomy, e.g. the number of antennal segments, the structure of the legs, the number of ocelli or simple eyes present, the number of setae on different organs, etc. These papers seldom contain important morphological details. In some of the older works, like those by Targioni-Tozzetti (1867), Wiltaczil (1886), Putnam (1878) and Schmidt (1885) serious attempts were made to elucidate the structure of male coccids, but probably because of the inadequacy of technical aids at that time, these descriptions are usually incomplete and some of their observations now appear to be inaccurate. To some extent this also applies to Berlese's papers (1893—96), but he studied the anatomy of male coccids in much more detail than any of his predecessors and most of his findings have, hitherto, not been queried. It is indeed unfortunate that subsequent investigators of the anatomy of male coccids did not follow the admirable example set by Berlese and tried to elaborate his work.

Much of Nel's work (1933) is only a repetition of Berlese's findings (and mistakes) and many of the details given in Stickney's paper (1934) are apparently inaccurate. Balachowsky's paper (1937) on the anatomy of male

coccids consists largely of a compilation of the facts known at that time and contributes very little new information, apart from his suggestions on the classification of male coccids. The paper by Mäkel (1942) on *Pseudococcus* is a very elaborate work on the anatomy of male coccids, but is more concerned with musculature than with external morphology. Recently Jancke (1955) published a paper on the morphology of male coccids, but in actual fact it contributes relatively little that is morphologically significant. Other publications in which the general anatomy of male coccids is described, are by Suter (1932), Geier (1949), MacGillivray (1921), Mahdihassan (1931), Morrison (1928), Pesson (1941), Oguma (1919), Misra (1931), Sulc (1932, 1943), etc. The structure of the eyes of male coccids was investigated by Kreckler (1909) and Pflugfelder (1936), and Misra (1939) studied the development of the male genitalia.

In the present investigation the wing venation was not studied as it is impossible to ascertain with any degree of certainty the homology of the veins, before more is known about their development. The brief note by Patch (1909) on the wing tracheation of *Dactylopius* is apparently the only information available on the subject.

Handlirsch (1908) regards the coccids as a separate sub-order but according to Ferris (1937) the family Coccidae should be raised to the rank of a superfamily, the Coccoidea, and all its former sub-families to family status. This interpretation by Ferris will be followed in all the subsequent discussions, although it also means regarding the other Sternorrhynchan families as superfamilies.

II. MATERIAL AND TECHNIQUE

The following representatives of various families were studied:

- (1) *Margarodes vitium* Giard (Fam. Margarodidae; subfam. Margarodinae). Collected on *Vitis vinifera* L. at Kakamas.
- (2) *Pseudaspidoproctus* (?) *fulleri* (Ckll.) (Fam. Margarodidae; subfam. Monophlebiniae). Collected on grass at Port Elizabeth.
- (3) *Steingelia gorodetskia* Nasonow (Fam. Margarodidae; subfam. Steingeliinae). Collected on *Betula verrucosa* Ehrh. at Sunninghill, Berkshire, England.
- (4) *Eulecanium taxi* Habib (Fam. Lecaniidae). Collected on *Taxus baccata* L. at Sunninghill, Berkshire, England.
- (5) *Pseudococcus citri* (Risso) (Fam. Pseudococcidae). Collected on *Vitis vinifera* L. at Stellenbosch.
- (6) *Aulacaspis pentagona* (Targ.) (Fam. Diaspididae; subfam. Diaspinae). Collected on *Ligustrum japonicum* at Pretoria.
- (7) *Diaspidiotus bavaricus* Lind. (Fam. Diaspididae; subfam. Aspidiotinae). Collected on *Calluna vulgaris* L. at Sunninghill Berkshire, England.

Because the body of the male coccid is more or less cylindrical and usually only very weakly sclerotized, it was found that the ordinary methods used in preparing female coccids for microscopic examination caused so much shrinkage that the specimens were almost useless. In the past the only means by which most workers have studied the males has been by whole mounts on slides, but this method proved to be quite unsatisfactory. It was found to be much more convenient to have the specimens submerged

in a fluid (terpineol) and examine them under the stereoscopic microscope, or, for more critical examination, to mount them temporarily in cavity slides. These methods prevent the specimens from being crushed and also permit of their being examined from all angles. Hitherto most workers have usually only studied permanent mounts showing the insect in dorsal or ventral view and for this reason the pleural region has never been properly studied.

After many trials the following method of preparing material for microscopic examination was specially developed and was found to be the most satisfactory:

Material was fixed in Carnoy-sublimate (Mäkel, 1942), consisting of 100 cc. Carnoy's fluid + 12 gm. corrosive sublimate, for 30 minutes. The sublimate was afterwards removed by treatment with iodine dissolved in alcohol and the specimens were then preserved in 70% alcohol.

To clear them, specimens were gently heated in 10% KOH solution until the internal organs were dissolved, then they were washed in distilled water and dehydrated by passing them slowly through a graded series of alcohols. From absolute alcohol they were transferred to a saturated solution of Chlorazol Black E in absolute methyl alcohol and left until the specimens were stained bluish. The excess stain was then removed by leaving them in absolute ethyl alcohol for a few hours. After that they were transferred gradually from alcohol to terpineol by means of the method described by Gray (1952). In using this method, terpineol is poured into a small dish and some absolute alcohol added carefully afterwards, so that the terpineol and alcohol form two separate layers. The specimens are then transferred to the dish and will at first float on the surface of the terpineol layer, but will sink very slowly to the bottom of the dish as the alcohol inside them is gradually replaced by terpineol; this gradual replacement prevents shrinkage. The alcohol is then poured off and the specimens transferred to fresh terpineol. Microscopic examination was carried out in terpineol.

Chlorazol Black E, which was first used by Cannon (1941) and which was described by Pantin (1948) as having strong affinities for chitin, was found to be excellent for staining male coccids as (1) it is not washed out in either alcohol or terpineol and (2) it gives a better differentiation between sclerotized areas and membrane than any of the conventional stains like Fuchsin or Congo Red.

Where it was necessary to study the musculature, the larger specimens were dissected in alcohol, but the smaller specimens were prepared as described by Weber (1928) i.e. bleached in diaphanol, stained in borax carmine, differentiated in acid alcohol and finally dehydrated. They were then embedded in ester wax and sectioned up to the median line with a microtome. The uncut half was then immersed in xylene to dissolve out the wax, and mounted on a slide. In this way the musculature of small specimens, like *Aulacaspis*, could be studied under high magnifications. Transverse and longitudinal serial sections were also cut of all the specimens, which were first embedded in ceresin wax and sectioned 6μ thick. Mallory's stain proved to be the most useful for staining the cuticle and muscles.

The drawings were all made from specimens which had been cleared in KOH and are therefore naturally slightly distended when compared with living specimens. All drawings were made to scale on graph paper by using a squared eyepiece micrometer. In all the drawings internal ridges are

indicated as thick black lines as wide as the ridge, sclerotized areas are stippled, and membranous areas are left blank. Where the limits of a sclerotized area were not very definite, as is often the case in weakly sclerotized areas, they were indicated by dots. Internal structures, or structures which could not be seen through overlapping by another structure, were drawn, where necessary in broken lines.

III. THE HEAD

A. GENERAL.

According to Weber (1928, 1935) the head of Homoptera consists of three distinct regions, the epicranium, "Vorderkopf" and labium. The epicranium is that part of the head bearing the antennae, eyes and ocelli, while the "Vorderkopf" consists of the clypeus, labrum and the mandibular and maxillary plates with their respective stylets. The mouth opening, sucking pump, hypopharynx, etc. also belong to the "Vorderkopf". The labium is usually partially fused with the prothorax and encloses the stylets.

As male coccids do not feed, the structures associated with this function are, with the exception of a vestigial, non-functional mouth opening and alimentary canal, completely absent. The head therefore consists mainly of the epicranium, which, because of the opisthognathous condition of the head, also stretches far back ventrally. The phenomenon called "sclerite degeneration" by Weber (1933) is also very pronounced and, by reducing sclerotized areas to narrow strips or ridges with large intervening membranous areas, further obscures the general structure of the cephalic region, whose interpretation is already rendered difficult by opisthognathy and the atrophy of structures.

B. *MARGARODES VITIUM*.

The head of *Margarodes* resembles that of other Homoptera in many respects but has never been adequately studied. Morrison (1928) and Jancke (1955) describe it only very briefly, giving almost no morphological details.

The head can be readily distinguished from the thorax as it is much narrower than the prothorax and a shallow cervical groove is also present. According to Weber (1928, 1929 and 1935a) a sclerotized area, the epicranium, bearing the compound eyes, ocelli and antennae, occurs in *Aphis*, *Psylla* and aleyrodids. In *Margarodes* more or less similar conditions prevail but, probably because of sclerite degeneration, the dorsal and ventral surfaces of the epicranium are separated from the lateral ones by membrane (Figs. 1, 2, 3). The epicranium therefore consists of:

- (i) a dorsomedial triangular plate (dmep) which is anteriorly continuous with a similar sclerotized area on the ventral surface of the head (vmep), and
- (ii) two lateral ocular sclerites (ocs) which bear the compound eyes and articulate posteriorly with the cervical sclerites. Ventrally the ocular sclerites are separated from the medial portion of the epicranium by membrane.

The compound eyes (e) are very large and are almost contiguous ventrally (Figs. 1, 3). Laterally behind each eye the ocular sclerite forms a distinct prominence bearing an ocellus-like structure (o), which closely resembles

the lateral larval eyes of *Aphis* (Weber, 1930; Pflugfelder, 1937). As larval eyes occur in the adult males of *Eulecanium* (Pflugfelder, 1936), it is almost certain that they also represent persisting larval eyes in *Margarodes*. These eyes may for convenience (see p. 19 for discussion) be called lateral ocelli. True dorsal ocelli seem to be completely absent and no trace of a median dorsal eye, comparable to that described by Jakubski (1929) in *Margarodes polonicus*, could be found.

Anterior to each compound eye the 10-segmented antenna is inserted in the membrane, its scape (scp) therefore lacks a sclerotized socket. Posteriorly the scape has a small basal process, to which one of the antennal muscles is attached, and distally it articulates with the pedicel (pdc) by means of a dorsal and ventral pivot. The scape and pedicel are short and globular, but the remaining segments of the antenna are elongate and approximately of equal length.

Near the posterior margin of the dorsomedial part of the epicranium (Fig. 1, dmep) is a suture with a strong internal ridge and the position of this suture on what is obviously the posterior margin of the head — there is a distinct membranous neck between the epicranium and the pronotum — immediately suggests that it corresponds to the post-occipital suture of aleyrodids (Weber, 1935a) and *Magiccicada* (Snodgrass, 1935). According to Snodgrass (1928) the two main criteria for the recognition of the postoccipital suture are:

- (a) the posterior tentorial pits are always located in its lower ends, and
- (b) the anterior ends of the dorsal muscles of the prothorax are attached to the postoccipital ridge.

The former criterion is ostensibly absent in *Margarodes* as this suture is in no way connected with the posterior tentorial pits, which have shifted very far ventrally. The pits are however still dorsoventrally in line with the suture, thus indicating that the detachment is probably a secondary one.

As regards the second criterion, it was found that three muscles are attached to the ridge (Fig. 4). Two of these (3 and 4) extend from the medial part of the ridge to the lateral portion of the mesoprephragma and are probably homologous with a similar muscle found in aleyrodids, where, according to Weber (1935a), a postoccipital ridge can be distinguished. Weber states that in aleyrodids this muscle originated from the fusion of a neck muscle between the postoccipital ridge and the pronotum with a muscle between the pronotum and mesothorax. It is possible that similar conditions obtain in *Margarodes* and that the ridge on the epicranium is therefore cephalic and not prothoracic, as these muscles extending between it and the mesothorax would suggest. In *Psylla* (Weber, 1929) and *Aphis* (Weber, 1928) the muscles stretching anteriorly from the mesoprephragma are attached to the anterior margin of the pronotum and there are distinct neck muscles between the pronotum and the posterior margin of the head. Separate neck muscles are absent in *Margarodes*. A third muscle (2) extends between the ridge and the cervical sclerite, thus having the same attachments as a similar muscle inserted on the postoccipital ridge in aleyrodids (Weber, 1935a).

In the light of the above evidence it seems therefore quite reasonable to assume that the suture near the posterior margin of the dorsomedial part of the epicranium in *Margarodes* is a postoccipital suture which is perhaps

degenerate laterally. Posterior to the suture there is a narrow sclerite which may be regarded as a postociput (poc), to which the neck membrane is attached.

Weber (1928) states that the epicranium in *Aphis* probably consists of both a vertex and a frons, but Snodgrass (1947) is of the opinion that in aphids the frons has been entirely obliterated. The medial part of the epicranium of *Margarodes* lacks all evidence of a division into a frons and vertex and extends far back ventrally, probably because of the opisthognathy of the head. Anteriorly between the antennae it narrows considerably, expanding again beyond the apex of the head (Fig. 2, vmep). Ventrally between the eyes, however, it is reduced to a narrow strip, bearing a very strong internal ridge for the attachment of three pairs of antennal muscles (Fig. 4, ant. mscls). This ridge, which will be termed the midcranial ridge (mcr), probably corresponds to the midcranial ridge or inflection which according to Du Porte (1946) persists in adult insects in the position normally occupied by the ecdysial cleavage line (coronal suture) of larvae. In *Psylla* there is a cephalic ridge almost identical with that of the midcranial ridge of *Margarodes* but Weber (1929) does not homologize it with any part of the epicranial suture.

The attachment of the antennal muscles to the midcranial ridge is an interesting phenomenon. According to Snodgrass (1928) the antennal muscles originally had their origin dorsally on the cranial wall, as they still have in some larval insects. Secondarily they then migrated from the cranial wall on to the dorsal and anterior arms of the tentorium, to which they are attached in most adult Pterygota. In the Auchenorrhyncha, according to Kramer (1950), they arise on the dorsal arms of the tentorium in Cicadidae, Cercopidae, Cicadellidae and Membracidae and on the tentorial bridge in the Fulgoridae. Among the Sternorrhyncha they are attached to the anterior tentorial arms in *Psylla* (Weber, 1929), aleyrodids (Weber, 1935a) and *Aphis frangulae* (Roberti, 1946). In *Aphis fabae* (Weber, 1928) on the contrary, only one of the antennal muscles arises on the anterior arm, while the other three have migrated to an apodeme on the posterior margin of the postclypeus. A dual attachment for the antennal muscles was also found in females of *Icerya* by Pesson (1944). In male *Margarodes* this migration of the antennal muscles has apparently progressed still further. They have completely abandoned the anterior tentorial arms and again become secondarily attached to a ridge on the cranial wall, thus almost reproducing the hypothetical primitive condition. The only difference is that, whereas primitively the cranial attachment of the muscles was supposed to be dorsal to the antennal socket, it is now ventral in *Margarodes*.

Posterior to the point of attachment of the antennal muscles, the midcranial ridge gradually fades out and the ventromedial part of the epicranium widens into a ventral plate (vp) on whose inner surface the anterior arms of the tentorium (ata) originate. The area behind the anterior pits must necessarily be regarded as the clypeal region, although there is no epistomal suture between the pits to delimit the postclypeus from the epicranial region. The ventral plate probably incorporates parts of the lateral and posterior cranial wall.

The posterior tentorial arms (Fig. 4, pta) are invaginated laterally from the membrane in two small incisions of the ventral plate. Both the

anterior and posterior tentorial arms are very delicate, flimsy structures and are connected with each other and the pair on the opposite side by a bandlike tentorial bridge (tb), which passes ventrally to the oesophagus. The tentorium thus closely resembles that of other Sternorrhyncha and of female margarodids like *Icerya* (Pesson, 1944). The tentorial bridge is connected dorsally to the anterior margin of the pronotum by means of a muscle [Fig. 4, (8)]. This muscle doubtless corresponds to the musculus secundus tentorii of *Aphis* (Weber, 1928) and *Psylla* (Weber, 1929).

The mouth opening (mo), which is devoid of mouth parts and therefore probably non-functional, is situated medially behind the ventral plate. Three muscles are attached laterally to the posterior margin of the ventral plate. One (5) extends dorsally to the post-tergite (pt) of the prothorax and therefore probably represents the musculus intersegmentalis labii of *Aphis* (Weber, 1928), which stretches between the labium and the post-tergite. The other two muscles (6 and 7) go to the prosternum and lateral cervical wall respectively and obviously correspond to the ventral labial muscles, stretching between the posterior margin of the head and the prothorax in *Aphis*, *Psylla* and aleyrodids (Weber, 1928, 1929 and 1935a). These muscle attachments seem to indicate either that the ventral plate of *Margarodes* also incorporates part of the labium, or that the labium is absent and the three muscles have become secondarily attached to the posterior edge of the ventral plate. Behind the ventral plate is a very large membranous area representing the neck and part of the prothorax.

C. PSEUDASPIDOPROCTUS (?)FULLERI.

Although *Pseudaspidopectus* is evidently closely related to *Margarodes*, its head shows some striking differences. Morrison (1928) gives almost no morphological details of cephalic structures in this genus.

Dorsally the head is incompletely sclerotized and largely membranous (Fig. 6). There is, however, a well developed postoccipital suture (pos) with a strong internal postoccipital ridge and narrow postocciput (poc), comparable with that of *Margarodes*. Anterior to the postoccipital suture only a small triangular portion of the dorsomedial part of the epicranium (dmep) is sclerotized, a broad membranous area separating it from the midcranial ridge (mcr).

Laterally the postoccipital ridge is connected to the ocular sclerites (ocs) by weakly sclerotized cuticle (Fig. 8). As in *Margarodes* each ocular sclerite bears a compound eye (e) and a lateral ocellus (o). An internal ridge, the postocular ridge (pocr) originates dorsal to the eye, runs down behind the ocellus and terminates on the ventral edge of the ocular sclerite, where it separates off a broad flat, strongly sclerotized projection (p).

Like *Margarodes* the 10-segmented antenna has no sclerotized socket. The basal part of the enlarged scape (scp) is heavily sclerotized and strengthened by two marginal ridges, which coalesce posteriorly to form a strong basal articular process. Distally it articulates with the pedicel by means of a dorsal and ventral process. The pedicel (pdc) is more slender, has a basal ridge and articulates ventrally with the scape by means of a well developed pivot-like process (Fig. 7). The segments of the flagellum are all very much alike although they become more slender towards the apex.

Ventrally the eyes are not as close together as in *Margarodes* and the ventromedial part of the epicranium (vmep) is therefore more extensive (Fig. 7). A midcranial ridge (mcr), similar to that of *Margarodes*, originates dorsally between the antennae and runs ventrally, where, unlike *Margarodes*, it is joined by a preocular ridge (procr), originating between the compound eye and the antenna. The preocular ridge articulates with the basal process of the scape as well as with a small process of the ocular sclerite anterior to the eye. Further back the midcranial ridge bifurcates, forming two preoral ridges (pror), which stretch far back ventrally.

In the absence of fronto-clypeal muscle attachments, which according to Snodgrass (1947) indicate the point of forking of the ecdysial suture, the homologies of the preocular and preoral ridges are rather obscure, but the preoral ridge shows some resemblance to the transfrontal sulcus, which Du Porte (1946) describes in nymphal *Magicalada*. The preocular ridge is more problematic, for although its course superficially agrees reasonably well with that of the frontal suture, the latter never coincides with a ridge-bearing sulcus (Du Porte, 1946). As these ridges definitely serve to support the extensive ventral surface of the head, to which the antennal muscles are attached, it may well be that they have developed secondarily for that purpose. A further indication of a probably secondary origin is that similar ridges are absent in the other Sternorrhynchan superfamilies, excepting perhaps the Aleyrodoidea, where a cuticular fold separates the compound eye from the antenna (Weber, 1935a). Until the ridgeforming sulci and the ecdysial line in the hemipteran head have been further investigated, it is therefore better to retain the purely topographical terms preocular and preoral for the ventral cephalic ridges of *Pseudaspidopectus*.

Immediately posterior to the point where the midcranial ridge forks to produce the preoral ridges, the epicranium is invaginated deeply to form a short broad heavily sclerotized apophysis (ca) for the attachment of the four pairs of antennal muscles. The anterior tentorial pits (atp) are situated on the posterior edge of this cranial apophysis and give rise to the anterior tentorial arms (ata). These are more delicate than the rather stout posterior tentorial arms (pta), which are invaginated from the membrane further posteriorly. The tentorial bridge (tb) is also very delicate and is connected to the anterior margin of the pronotum by a pair of weak muscles, identical with muscle (8) of *Margarodes*. As in *Margarodes* the topographically anterior margin of the clypeus is not delimited by a suture between the anterior tentorial pits; a ventral plate is absent.

Between the posterior extremity of the preoral ridge and the posterior tentorial pits, a pair of small separate triangular sclerites (vs) is found in the membrane. When this part of the head is compared with that of *Margarodes*, it immediately becomes apparent that these ventral sclerites represent detached portions of the ventral plate (vp), resembling, to some extent, similar sclerites found in *Aphis* (Weber, 1928). As the ventral sclerite is situated in front of the posterior tentorial pit, it obviously cannot be regarded as a cervical sclerite. A strong muscle, extending to the postoccipital ridge is attached by means of a tendon-like apodeme (t), which is not destroyed by KOH, to the medial edge of the ventral sclerite. The homology of this muscle is obscure, but its attachment to the post-occipital ridge suggests that it may be the musculus tentorii primus which has shifted

secondarily from the tentorium. In *Aphis*, *Psylla* and *Aleyrodoidea* (Weber, 1928, 1929, 1935a) the musculus tentorii primus extends from the postoccipital region to the tentorial bridge. This muscle is definitely absent in *Margarodes* and cannot be regarded as homologous with muscle (2) of that genus (Fig. 4) as a muscle stretching between the postoccipital ridge and the cervical sclerite is also present in *Pseudaspidopectus*. No other muscles are inserted on the ventral sclerite, the dorsoventral and longitudinal intersegmental muscles being attached to a membranous fold posterior to the sclerite.

The mouth opening (mo) is situated on a conical projection between the preoral ridges (Fig. 8) and internally has a small cavity which perhaps represents a vestigial cibarium. Immediately posterior to the mouth opening the duct (sd) of what in serial sections appears to be the salivary gland, opens externally. Further posteriorly a large membranous area is found and the posterior margin of the head is only indicated by an incision which apparently represents the cervical groove.

D. *STEINGELIA* GORODETSKIA.

The genus *Steingelia* is included in the family Margarodidae by most workers on that group, e.g. Green (1914), MacGillivray (1921), Morrison (1928), Pflugfelder (1939), Balachowsky (1948), etc., female structures forming the basis for their classification. The head of the male, however, differs from that of other margarodid males in so many respects that Green (1917) suggests the removal of this genus from the Margarodidae. In a later work (1920) he states that the male characters of *Steingelia* seem to constitute a connecting link between the Margarodidae and the Pseudococcidae. This statement will receive further consideration on p. 59.

There can be little doubt that the head of male *Steingelia* is highly specialized. Except for some strong internal ridges, it is relatively weakly sclerotized and the sclerotized areas are not as well defined as in *Margarodes* and *Pseudaspidopectus*. Apart from the midcranial ridge (mcr), which extends back to the occipital region, the dorsal surface of the head between the ocular sclerites (ocs), is completely membranous (Fig. 9). A postoccipital suture and ridge is not developed and the muscles which are normally attached to the latter, are inserted on the widened posterior extremity of the midcranial ridge.

The ocular sclerites are bulbous, slightly sclerotized and occupy the whole of the lateral aspects of the head. They are contiguous ventrally and there are no postocular ridges along their posterior edges (Fig. 11). In addition to a lateral ocellus (o), comparable with that of *Margarodes* and *Pseudaspidopectus*, each ocular sclerite bears an anterior row of 7 simple eyes (se) surrounded by membrane and occupying the same position as the compound eye in *Margarodes* and *Pseudaspidopectus*. These simple unicorneal eyes probably represent a modified compound eye, a view expressed by MacGillivray (1921) and also endorsed by Morrison (1928) and Weber (1935b). Research by Pflugfelder (1936) on the structure and development of the eyes in *Eulecanium corni*, led him to support this view also.

The scape (scp) of the antenna is inserted in the membrane anterior to the ocular sclerite and possesses a basal ridge with a posterior articular process. Only the ventral surface of the scape is sclerotized and gives rise

to a process articulating with the ridge which surrounds the base of the sclerotized pedicel (pdc) ventrally but not dorsally. The flagellum consists of 8 rather similar, elongate segments.

The midcranial ridge (mcr) extends anteriorly and over the apex of the head, from the occipital region and fades out in a small sclerotized protuberance (vmep) on the lower part of the front of the head (Fig. 11). The latter is the only recognisable part of the ventromedial portion of the epicranium. When the midcranial ridge reappears beyond the protuberance, it is joined immediately by the very much flattened, heavily sclerotized preocular ridges (procr), which articulate with the pivot-like process at the base of each scape. The preocular ridges are not visible externally because they are located in deep folds of the membrane anterior to the ocular sclerites. As in *Pseudaspidopectus* the midcranial ridge is continued posteriorly as a thick ridge, but owing to the fact that the ocular sclerites are contiguous ventrally for a considerable distance, it is covered by the latter and, for that part of its course, is therefore not externally visible. Near the point where it again becomes superficially visible (Fig. 10), the cranial apophysis, to which the four pairs of antennal muscles are attached, is invaginated from the ridge. The cranial apophysis is fairly long, armlike and heavily sclerotized.

Further back the midcranial ridge bifurcates, giving rise to the preoral ridges (pror) which diverge at first but then converge until they almost meet near the mouth opening. The preoral ridges of *Steingelia* differ from those of *Pseudaspidopectus* in that they originate posterior to the point where the cranial apophysis is invaginated. They also extend much further posteriorly — almost to the anterior tip of the prosternum. The anterior and posterior arms of the tentorium are invaginated very far back on the edges of the preoral ridges. The tentorial arms are long and flimsy, stretching posteriorly to the precincts of the mesothorax, where the arms of the opposite sides are connected to each other by the long thin suboesophageal tentorial bridge (tb). No muscles attached to the tentorium could be found by dissection or the study of serial sections. This region of the head of *Steingelia* is obviously very specialized and there has been a pronounced caudal migration of structures. A sclerotized clypeal region or ventral plate is completely absent. The head of *Steingelia* appears to be more opisthognathous than that of *Margarodes* and *Pseudaspidopectus*.

E. *EULECANIUM TAXI*.

The lecaniid head has been described and figured by Green (1904—09), Silvestri (1920), Sulc (1932) and Dürre (1954) but all these papers contain few significant morphological details and little more than the number and disposition of the eyes of different species can be ascertained from them. Pflugfelder's important paper (1936) on the structure and development of the eyes in *Eulecanium corni*, is however a major contribution to our knowledge of the visual organs in male coccids.

Dorsally there is no postoccipital suture and the mesothoracic muscles are attached to the posterior tip of a slightly elevated median sclerotized area, representing the dorsomedial part of the epicranium (Fig. 12, dmep). The posterior margin of this sclerotized area probably does not coincide with the

position which the postoccipital ridge would normally have occupied, the cervical indentation indicating that the points of attachment of the mesothoracic muscle have probably migrated anteriorly. The dorsomedial part of the epicranium stretches anteriorly over the apex of the head, ending between the antennae, where it meets the midcranial ridge (Fig. 13, mcr). At the point of junction the midcranial ridge on each side sends out a lateral branch (lmcr) in the direction of the base of the scape without, however, articulating with it. The midcranial ridge has a similar course in *Pulvinaria mesembryanthemi* where Pesson (1941) calls it a "chitinous impression". Postero-ventrally the midcranial ridge ends in a small transverse sclerotized area, which lies in line with a ridge running between the dorsal eye and the antenna (Fig. 14). As this ridge also has a process for articulation with the base of the scape, there can be little doubt that it represents the preocular ridge (procr) of *Pseudaspidopectus*.

A strip of membrane separates the dorsomedial part of the epicranium from the ocular sclerites (ocs), which, in comparison with *Steingelia*, occupy a smaller portion of each cranial wall. Posteriorly each ocular sclerite is bounded by a strong ridge (pocr) which originates dorsally behind the eye and runs down posterior to the ocellus, terminating ventrally near the anterior tip of the cervical sclerite + pleuron (plev). It thus has the same relationships as the postocular ridge of *Pseudaspidopectus* and can be regarded as homologous with that ridge. Jancke (1955) mentions this ridge in *Physokermes piceae* and it is also described by Pesson (1941) in *Pulvinaria*. Anteriorly the ocular sclerite is partially bounded by the preocular ridge and ventrally the ocular sclerites of opposite sides are fused between the ventral eyes. Membrane separates the ocular sclerites from the preoral ridges.

Each ocular sclerite (ocs) bears an ocellus (o) and the simple unicorneal dorsal and ventral eyes are each surrounded by a narrow strip of membrane (Fig. 14). According to Pflugfelder (1936) the ocelli of *Eulecanium* represent persisting larval ocelli and will here be called lateral ocelli (see p. 19). Moulton (1907) also calls them larval eyes in *Psysokermes insignicola*. By studying the innervation and development of the simple dorsal and ventral eyes, Pflugfelder came to the conclusion that, in spite of the fact that each eye only has a single cornea, they represent modified compound eyes and are not dorsal ocelli. According to Sulc (1932), who makes no distinction between the simple eyes and the ocelli, some lecaniids have up to three smaller additional simple eyes laterally between the dorsal and ventral eyes. Green (1904—09) calls the simple eyes ocelli and the ocelli rudimentary eyes.

The antennae are inserted low down on the front of the head. They are 10-segmented, the scape and pedicel being globular but the other segments elongate. The scape (sep) is only dorsally sclerotized and is surrounded by a strong basal ridge which not only articulates with the preocular ridge, but also, by means of a rather lengthy ventral projection, with a process on the basal ridge of the pedicel. This ridge surrounds the pedicel (pdc) ventrally but is discontinuous dorsally.

As the ventral eyes are situated on two spherical extensions of the head capsule, there is a fairly deep groove between them (Fig. 13). Further back this groove leads to a deep sclerotized cavity (vc) from which both the cranial apophysis and the anterior tentorial arms are invaginated. The preoral ridges originate in front of this cavity and run backwards along its edges, even-

usually fusing with the postocular ridges. The cranial apophysis (ca) is relatively long and flattened, broadening towards the tip, where it is slightly forked (Fig. 22). Four antennal muscles are attached to each arm of the fork.

The anterior tentorial arms (ata) are well separated from one another where they originate within the ventral cavity posterior to the cranial apophysis (Fig. 22). They are fairly stout and are joined posteriorly by the much more slender posterior tentorial arms (pta), which originate medially to the posterior curved ends of the postocular ridges. The tentorial arms of opposite sides are joined together by the tentorial bridge (tb), which is heavily sclerotized. Generally speaking the tentorial arms of *Eulecanium* are much shorter than those of *Margarodes*, *Pseudaspidopectus* and *Steingelia* and the tentorium therefore has a much greater resemblance to the typical homopteran tentorium.

On each side a muscle, extending to the posterior edge of the dorsomedial part of the epicranium, is attached to the postocular ridge by means of a strong tendon-like apodeme (t), which is not destroyed by treatment with KOH. There can be little doubt that these two muscles, with their apodemes, are homologous with similar structures in *Pseudaspidopectus*, especially as the apodemes are also attached to the cranial wall about halfway between the anterior and posterior tentorial pits.

The mouth opening is situated in the membrane immediately behind the ventral cavity and the oesophagus runs dorsal to the tentorial bridge. A large area behind the mouth opening is membranous and the posterior margin of the head is indicated by the deep cervical groove.

F. *PSEUDOCOCCUS CITRI*.

The head of *Pseudococcus* has been described by both Berlese (1893) and Mäkel (1942). Berlese's paper gives few morphological details, but Mäkel's paper, although primarily concerned with musculature, gives many details of cephalic structures. The papers by Vaney and Conte (1908), Cottier (1936) and Jancke (1955) contribute little of morphological value.

Dorsally there is no distinct postoccipital ridge but only two short narrow meniscate ridges to which the muscles, normally associated with the postoccipital ridge, are attached (Fig. 15). From these ridges a triangular sclerotized area, the dorsomedial part of the epicranium (dmep), extends anteriorly, ending between the antennae in a short median ridge which must be regarded as a detached dorsal portion of the midcranial ridge (mcr). The ventral extension of the midcranial ridge is completely separated from this short dorsal part, but as in *Eulecanium* it gives off two branches (lmcr) to the bases of the antennae. These branches do not articulate with the base of the scape. The midcranial ridge does not extend far ventrally and disappears in front of the eyes. The so-called frontal apophysis, which according to Berlese (1893) originates anteriorly between the antennae and to which antennal muscles are attached, does not exist in *Pseudococcus citri* and he must have mistaken the ventral portion of the midcranial ridge for an apophysis. No antennal muscles are attached in this region. Sulc (1943) describes a cruciform structure in the dorsal region of the head of *Phenacoccus aceris*.

The ocular sclerites (ocs) are dorsally very narrow compared with *Steingelia*, and they are bounded posteriorly by ridges which Mäkel (1942)

refers to as the dorsal and the ventral branches of two ridges which bifurcate below the ocelli (Fig. 17). These ridges clearly correspond to the postocular ridges (pocr) of *Pseudaspidoproctus* and *Eulecanium* as they have the same relationships to neighbouring structures. Berlese (1893) describes the postocular ridges in *Pseudococcus citri* without naming them, but his description is inaccurate as he considers them to be connected with each other and dorsally with the posterior margin of the head. Membrane separates the dorsomedial part of the epicranium from the ocular sclerites. Behind each postocular ridge is also a large rounded membranous area, extending up to the cervical groove.

Each ocular sclerite is bounded anterodorsally by a ridge which eventually fuses with the postocular ridge (Fig. 17). When compared with conditions in *Eulecanium*, it is quite clear that this ridge must be the preocular ridge (procr) which cuts across the ocular sclerite ventral to the point where it articulates with the scape, and fuses with the postocular ridge below the ocellus. Sulc (1943) describes in *Phenacoccus*, "paraocular bars", which enclose sclerotized areas between them and obviously correspond to the pre- and postocular ridges. The posterior one of these "paraocular bars" is also called the postocular bar by him. Anteroventrally the ocular sclerites are not bounded by ridges and they are indistinguishably fused with one another ventromedially (Fig. 16). Posteroventrally the ocular sclerites are bounded by the preoral ridges (pror).

As in *Eulecanium taxi* each ocular sclerite bears a pair of large dorsal and ventral simple eyes and a pair of lateral ocelli. The ventral eyes are situated on two conical prominences, with a groove between them. Berlese (1893) called the simple dorsal and ventral eyes of *Pseudococcus*, accessory eyes and the ocelli, lateral eyes. He also states that the ocelli (lateral eyes) are the larval eyes which persist in the adult. Kreckler (1909) calls the ocelli primary eyes in *Pseudococcus (Dactylopius)* and the simple eyes accessory eyes after Berlese. By studying the development of the eyes he found that the simple ventral eyes do not occupy the position of the mouth parts, as has been stated by some authors, but that the ventral eyes begin to develop when the mouth opening is still present. This observation could, however, also have been made by examining only the adults, where the vestigial mouth opening is still present well behind the ventral eyes.

The antennae are inserted in the membrane almost directly in front of the ocelli. The scape (scp) is sclerotized dorsally and ventrally and its basal ridge lacks a projection for articulation with the preocular ridge. Ventrally the scape has a distinct distal process for articulation with the basal ridge of the pedicel (pdc). As in *Eulecanium* this ridge is developed ventrally but not dorsally.

When the above description of the ridges on the head of *Pseudococcus* is compared with that given by Mäkel (1942), a number of differences are immediately apparent. The dorsal U-shaped ridge, which she describes, is actually non-existent and there is no connection between the preocular ridges and the two small meniscate dorsal ridges at the posterior end of the sclerotized dorsomedial part of the epicranium. The broad heavily sclerotized ring surrounding the ocellus, which is described by her and figured by Weber (1930), is also absent. Furthermore there is no continuous median ridge running from the meniscate sclerites to the vicinity of the ventral eyes. She

describes neither the two branches of the midcranial ridge running to the bases of the antennae, nor the lightly sclerotized areas of the head.

In contrast to *Eulecanium*, the ventral cavity (vc), from which the cranial apophysis and the anterior tentorial arms are invaginated, has in *Pseudococcus* been reduced to a mere slit whose external opening is situated behind the ventral eyes (Fig. 16). The cranial apophysis (ca) is dorsoventrally flattened and fairly short and according to Mäkel (1942), four pairs of antennal muscles are attached to it. Berlese (1893) who recognized this apophysis, describes the antennal muscles attached to it and calls it the occipital apophysis. As this structure is however very far removed from the occipital region, this term is misleading and cannot be retained.

The anterior tentorial arms (ata) originate posterior to the cranial apophysis, but because the ventral cavity from which they are invaginated is so narrow, the anterior tentorial pits have merged and the arms are therefore fused for a short distance (Fig. 23). Although the anterior tentorial arms are quite definite structures, they are extremely fine and therefore not easily recognized. Mäkel (1942) failed to find them and because of this, her interpretation of the structure and homologies of the cranial apophysis and the ventral cranial wall is partly erroneous. According to her, both the anterior tentorial arms and the postclypeus are incorporated in the cranial apophysis. However, as separate anterior tentorial arms are present and as the cranial apophysis originates in front of the anterior tentorial pits the participation of these structures in the formation of the cranial apophysis seems unlikely. When compared with conditions in *Pseudaspidopectus* and *Eulecanium* it is quite clear that the cranial apophysis of *Pseudococcus* is also only a simple invagination of the ventral epicranial wall.

The anterior tentorial arms are posteriorly fused with the posterior tentorial arms (pta) which are much stouter and are invaginated from the membrane medially to the posterior extremities of the postocular ridges. The arms of opposite sides are connected by means of the strong, arcuate tentorial bridge (tb). The preoral ridges (pror) extend from the posterior edge of the ventral cavity and fuse with the postocular ridges. The mouth opening is situated in the membrane between the preoral ridges.

According to Mäkel (1942) the cervical groove cannot ventrally be regarded as the posterior margin of the head, as she contends that parts of the so-called "Vorderkopf", and especially the labium lie behind this groove. I do not agree with this view. Firstly, the mouth opening is situated well in front of the cervical groove, thus indicating that the head of *Pseudococcus* is not nearly as opisthognathous as Mäkel would suggest and it is therefore very unlikely that parts of the head should extend posteriorly almost as far as the front coxae, as her schematic figure of the head of *Pseudococcus* indicates. Secondly, the muscle attachments, on which she bases her conclusions on the extent of the labium, are not very reliable criteria as they are subject to migration. In male coccids there is therefore much variation in the musculature of this region of the head. Furthermore, as the labium is definitely not sclerotized and very probably has become completely atrophied in conjunction with the other mouthparts, it is rather futile to speculate about the limits of a structure whose presence cannot even with certainty be recognized.

G. AULACASPIS PENTAGONA.

The heads of various Diaspididae have been described in a number of papers, but most of these descriptions are brief and divergent systems of nomenclature for the cephalic structures have unfortunately been used by different authors.

The head of *Aulacaspis* shows some striking differences from that of the male coccids described so far, particularly in its intimate union with the prothorax and the almost complete lack of sclerotized areas, apart from the ridges. Dorsally the head has a characteristic unsclerotized median crest (mc) (the raised area in *Parlatoria blanchardi*, Stickney, 1934) which is bounded posteriorly by a groove extending laterally and ventrally for some distance (Fig. 18). A strong ridge (por) coincides with this groove for a short distance across the midline and gives off two short anterior branches, which run along the sides of the crest. Immediately behind the narrowed posterior margin of the crest, this ridge forms a phragma-like internal projection to which two pairs of muscles, (3) and (4), extending to the mesoprephragma, are attached (Fig. 21).

This transverse ridge in the caudal region of the head of Diaspididae has received from workers on this group a variety of names. Targioni-Tozzetti (1876) describes a pigmented mass in this region but no ridge. Berlese (1896) calls this ridge in *Aspidiotus limonii* the posterior branch of the dorsal sclerotized ridges of the head and correctly describes the prothoracic muscles which are medially attached to it. Nel (1933) calls it the cephalic ridge in *Aonidiella* and Stickney (1934) simply describes it as the sclerotic area in *Parlatoria*. Geier (1949) writes about the anterior rim of *Epidiaspis leperii*.

The general position of this ridge and especially the fact that the prothoracic muscles, homologous with (3) and (4) of *Margarodes*, are attached to it, strongly suggests, however, that it represents the postoccipital ridge. Further evidence for this assumption is afforded by the fact that a muscle, comparable to (2) of *Margarodes*, extends between the lateral extremity of this ridge and the cervical sclerite + pleuron (Fig. 21). Near the point where this muscle is attached, another muscle (9) is inserted and as it extends to the ventral surface of the head, it may be homologous with the muscle which in *Pseudaspidopectus* and *Eulecanium* is attached to the postoccipital region on one side, and by means of a tendon-like apodeme to the ventral wall of the head capsule on the other side.

It is quite clear that the transverse groove which is found behind the dorsal eyes and the median crest does not represent the posterior margin of the head, as part of the postoccipital ridge is situated behind it. That part of the head lying laterally between the groove and the postoccipital ridge is called the gena (g) by Berlese (1896) and Green (1896—99).

Anteriorly the medial crest is bounded by a V-shaped ridge whose stem is continued anteriorly over the apex and down the front of the head for some distance (Figs. 18 and 20). This ridge obviously corresponds to the midcranial ridge (mcr) with its two lateral branches (lmcr), which is found in *Eulecanium* and *Pseudococcus*.

As in *Pseudococcus* a pair of simple dorsal and ventral eyes are present on rounded prominences, but the so-called lateral ocelli are apparently

absent. This is in accordance with the findings of Green (1896—99), who states that in the Diaspididae the lateral ocelli (which he calls rudimentary eyes) sometimes seem to be entirely suppressed. Stickney (1934) also found no ocelli in *Parlatoria*.

A strong ridge originates immediately posterior to the dorsal eye and runs down along the side of the head, terminating ventrally in the vicinity of the mouth opening (Fig. 20). This ridge undoubtedly represents the postocular ridge (pocr) and has been described by a number of authors. Berlese (1896) calls it the malar ridge in *Aspidiotus* and this term is also used by Nel (1933) for a similar ridge in *Aonidiella*. Stickney (1934) calls it an undetermined sclerite in *Parlatoria* and in *Epidiaspis*, Geier (1949) described it as the transverse frontal suture. It is also described in *Chionaspis salicis* by van Dinter (1950) and *Diaspis calyptroides* by Reali (1954). Three muscles are attached to the ventral part of the postocular ridge (Fig. 21). Two of these extend to the prosternum (stn) and are probably homologous with (6) and (7) of *Margarodes*. The third muscle runs dorsally and is attached to the lateral wall of the prothorax, thus resembling (5) of *Margarodes*. These muscles were also found in *Aspidiotus* by Berlese (1896).

A short ridge with a process articulating with the scape of the antenna is also found anterior to the dorsal eye (Fig. 20). It obviously corresponds to the preocular ridge (procr) and is not visible laterally because it is concealed by a fold anterior to the eye. From their descriptions and figures it is quite clear that both Berlese (1896) and Reali (1954) regard the preocular ridges as being connected with the postoccipital ridge dorsally, thus giving rise to the X-shaped structure which they describe in the *Diaspididae*. In *Aulacaspis* there is no trace of such a structure and it is very possible that these authors have in some instances mistaken the lateral edges of the median crest for ridges, a mistake which can easily be made when the head is only seen in dorsal view. The preocular ridge and the lateral branch of the midcranial ridge approach one another very closely, but there is definitely no connection between them. As the region between the pre- and postocular ridges are apparently not sclerotized, an ocular sclerite cannot be distinguished laterally.

The scape (scp) of the antenna is attached to the membrane in front of the eyes. As usual the scape has a strong basal ridge which articulates with the basal ridge of the weakly sclerotized pedicel (pdc) by means of a very well developed elongate ventral process. The scape is slightly sclerotized both dorsally and ventrally. The flagellum consists of 8 rather similar elongate segments.

A narrow sclerotized strip, obviously affording a firm base for the attachment of the dorso-ventral muscles (9) (Fig. 21), is found medially behind the ventral eyes (Fig. 19). This small sclerite (ocs) is apparently all that is left of the fused ocular sclerites. Immediately posterior to this sclerite, is the external opening (cao) of a long finger-like apophysis (ca) to which three pairs of antennal muscles are attached (Fig. 21). It is slightly forked at the tip and is evidently homologous with the cranial apophysis previously described in other male coccids. Berlese (1896) calls it the occipital apophysis in *Aspidiotus*, but conditions in *Pseudococcus*, etc. show that this structure is so far anterior to the occipital region that this term

is best discarded. Nel (1933) calls it the ocular apophysis, but he describes it as a ridge in *Aonidiella*. Stickney (1934) describes this invagination as the "furca of the head" in *Parlatoria* and Suter (1932) calls it a fold in the body wall of *Lepidosaphes ulmi*. The preoral ridges are altogether absent in *Aulacaspis*.

The antennal muscles, which are inserted on the cranial apophysis are all attached to the basal ridge of the scape in *Aulacaspis*, as they are in all other male coccids examined. Berlese's (1896) statement that one of the muscles extends to the base of the pedicel in *Aspidiotus*, is therefore probably incorrect. According to Suter (1932) there are two pairs of antennal muscles attached to the cranial apophysis in *Lepidosaphes*. In *Aulacaspis* no trace of the anterior and posterior tentorial arms could be found and it must be assumed that the whole of the tentorium has disappeared completely.

Immediately behind the external opening of the cranial apophysis, the tubercle (mt) on which the mouth opening is situated, is found (Fig. 19). The tubercle is flanked on both sides by two narrow sclerotized areas of unknown homology (s). Berlese (1896) regards this tubercle in the *Diaspididae* as the rudiment of a primitive rostrum. Geier (1949) apparently mistakes the vestigial oesophagus for the duct of a gland when he states that in *Epidiaspis* there is an integumentary gland with a fine duct occupying the position of the vanished mouth parts.

H. *DIASPIDIOTUS BAVARICUS*.

The head of *Diaspidiotus* is very similar to that of *Aulacaspis* in most respects. It is however more flattened dorso-ventrally and is so intimately joined to the prothorax that nearly all signs of a boundary between the head and thorax have been obliterated.

A strong transverse postoccipital ridge (por) is found dorsally behind a median crest (mc) which is less well developed than in *Aulacaspis* (Fig. 24). Laterally on each side of the crest a narrow sclerotized strip, comparable to the anterior projections of the postoccipital ridge in *Aulacaspis*, stretches anteriorly to between the dorsal eyes. A structure somewhat resembling the X-shaped ridge which Berlese (1896) describes in *Aspidiotus*, is thus formed. The postoccipital ridge also has a median internal phragma-like structure for the attachment of the prothoracic muscles.

The postocular ridge (pocr) is not visible dorsally as it is covered by a fold, but it is well developed and distinct laterally and ventrally, having a short posterior extension at its ventral tip (Fig. 26). In contrast to *Aulacaspis* an ocellus (o) is present laterally behind the postocular ridge, in addition to the simple dorsal and ventral eyes (accessory eyes of Berlese, 1896). This ocellus is very degenerate, lacks a cornea and has the appearance of a translucent bead-like lateral projection of the body wall, much resembling the ocelli of *Aonidiella* (Nel, 1933) and *Aspidiotus* (Berlese, 1896).

The preocular ridge (procr) is short and is not visible laterally because it is hidden by a fold (Fig. 27). It has no special pivot-like process for articulation with the basal ridge of the scape. Berlese's (1896) figures give the impression that the preocular ridge, which he does not describe, is fused to the anterior projection of the postoccipital ridge in *Aspidiotus*, but this is definitely not the case in *Diaspidiotus*. As in *Aulacaspis* the area between

the preocular and postocular ridges is not sclerotized and an ocular sclerite is therefore not recognisable.

The basal ridge of the scape (scp) is apparently only developed ventrally, where it possesses a strong pivot-like process articulating with the basal ridge of the pedicel (pdc). A large portion of the scape and the whole of the pedicel is weakly sclerotized. The flagellum is 8-segmented. The midcranial ridge (mcr) originates dorsally between the antennae, is not heavily sclerotized and lacks the lateral branches which are found in *Eulecanium*, *Pseudococcus* and *Aulacaspis*.

The external opening (cao) of the cranial apophysis is situated medially, well behind the ventral eyes and from it two weak ridges extend backwards in the direction of the tips of the postocular ridges (Fig. 26). These weak ridges probably represent the preoral ridges (pror) of other male coccids, but they appear not to be connected to the postocular ones as Berlese (1896) and Nel (1933) found in *Aspidiotus* and *Aonidiella* respectively. Apically the cranial apophysis (ca) is also slightly forked, but it is much shorter than in *Aulacaspis*. Three pairs of antennal muscles are attached to it. As in *Aulacaspis* the tentorium is altogether absent.

The mouth opening is situated relatively far back on a small tubercle (mt). A small sclerite (s), similar to that of *Aulacaspis*, is found on each side anterolateral to the mouth tubercle.

I. DISCUSSION.

According to Spooner (1938) and Evans (1941) the structure of the head capsule is of the greatest importance in determining the affinities of different groups of Homoptera and Heteroptera. This was also found to be true for male coccids. Compared with other Sternorrhynchan Homoptera the head of *Margarodes*, which is the most primitive of the male coccids studied, is very specialized in many respects. The most important of these are:

- (a) The loss of functional mouth parts and all of the accompanying musculature. This has changed the whole structure of the head profoundly.
- (b) The complete separation through sclerite degeneration of the median part of the epicranium from the lateral parts bearing the compound eyes and ocelli.
- (c) The undivided condition of the epicranium, i.e. the vertex and frons are not separated.
- (d) The migration of the antennal muscles from the tentorium to the ventral cranial wall.
- (e) The presence of a single pair of prothoracic muscles extending from the mesoprephragma to the postocciput, in place of two pairs in other forms.
- (f) The loss of the dorsal ocelli.

The general relationships between the coccid head and that of other Sternorrhyncha, will be discussed after the structure of the thorax and abdomen have been described.

Apart from the generally specialized condition of the primitive coccid head in comparison with that of other Homoptera, varying degrees of specialization are also apparent within the superfamily Coccoidea itself. A conspicuous feature is the varying degree of fusion between the head and

thorax. The head of *Margarodes* and *Pseudaspidopectus* is about as well separated from the thorax as that of aphids and aleyrodids. From this primitive condition two types of specialization have apparently evolved. In the first one the head becomes relatively more detached from the thorax through the development of a deep cervical incision or groove. A distinct, constricted neck region is thus formed. This condition is typical of *Steingelia*, *Eulecanium* and *Pseudococcus* and seems to be accompanied by the degeneration of the postoccipital suture and ridge. In the second type of specialization just the opposite happens and the junction between the head and thorax becomes so intimate that the boundary between these is almost completely obliterated. This condition is found in *Diaspidiotus* and to a lesser extent in *Aulacaspis*. There can be little doubt that both these conditions are specialized and Mäkel's (1942) contention that the fusion between the head and thorax in diaspid males is a primitive feature, because it simulates conditions in the larval stages, is unconvincing in view of the generally specialized nature of the larva.

The amount of sclerite degeneration that has taken place, is also an approximate indication of specialization. It is quite clear that the head of *Margarodes* is more sclerotized than that of any of the other species studied, as the median part of the epicranium is well sclerotized both dorsally and ventrally. In *Pseudaspidopectus* the head is heavily sclerotized on the ventral side only. In the others the heads are all much less sclerotized and the sclerotized areas are not well delimited, except where they are demarcated by ridges. Sclerite degeneration reaches an extreme in the Diaspididae, where even the circum-ocular regions are membranous.

Sclerite degeneration obviously also necessitated the development of secondary ridges for reinforcing the head capsule. As might be expected, secondary ridges are entirely absent in *Margarodes* (the midcranial ridge is regarded as primary) but are well developed and the only means of support for the head capsule in the highly specialized, largely membranous heads of the Diaspididae.

It is desirable to comment on the relationships between the large compound eyes of *Margarodes* and *Pseudaspidopectus*, the simple unicorneal eyes of other genera, and the so-called 'ocelli' which may exist alongside either of the first two. From Pflugfelder's (1936, 1937) work on the nervous connections and the development of the eyes of *Eulecanium*, it seems that the row of simple eyes in *Steingelia* and some lecaniids and the dorsal and ventral eyes of *Pseudococcus*, *Aulacaspis* and *Diaspidiotus* are all homologous with the compound eyes of other insects (including those of *Margarodes* and *Pseudaspidopectus*). The so-called lateral ocelli of the adult were shown by Pflugfelder to be the persistent ocelli of the larvae, and these in turn must be regarded not as homologues of the dorsal ocelli of some exopterygote nymphs (which are apparently absent from all Coccoidea), but as corresponding to a surviving group of ommatidia of the compound eye of more primitive exopterygote nymphs, a fact demonstrated by their structure and innervation. In more typical exopterygotes, the ommatidia of the nymphal eye become incorporated into the adult eye after being supplemented by the differentiation of further ommatidia. In most Coccoidea, and also in typical Aphidoidea, three nymphal ommatidia, which form the so-called lateral ocellus, remain separate from the further ommatidia which differentiate to form the simple

or compound eyes of the adult. Phylogenetically, therefore the "lateral ocelli", compound eyes and simple eyes of the adult are all equivalent and MacGillivray (1921) is to this extent justified in grouping ocelli and simple eyes together as "ocellanae". Ontogenetically the 'ocelli' are peculiar in that they are the only ommatidia to have developed fully during the pre-adult stages. The degeneration of the lateral ocelli of the Diaspididae must therefore be regarded as a specialized condition.

The development of the cranial apophysis is another very specialized feature and the absence of this structure in *Margarodes* is probably another indication of the relatively non-specialized condition of this genus. In *Pseudaspidopectus* the cranial apophysis is fairly rudimentary, but it reaches its maximum development in *Aulacaspis* and *Diaspidiotus*. In *Eulecanium* and *Pseudococcus* the anterior tentorial arms become secondarily associated with the cranial apophysis because the area on which both arise is invaginated to form the ventral cavity. The tentorium of *Margarodes*, *Pseudaspidopectus* and *Steingelia* can be regarded as primitive because it is not thus associated with the cranial apophysis. *Aulacaspis* and *Diaspidiotus* have secondarily lost the tentorium.

In conclusion it may be said that the structure of the head of the male coccids studied is far more homogeneous than is evident at first sight. In spite of a number of specializations, parts can generally be homologized fairly easily within the superfamily, and as so many similar specializations are found in widely different species, one is perfectly justified in assuming, on the basis of the structure of the head alone, that this group is monophyletic. Further conclusions about the possible inter-relationships of the species studied will be given after the additional information, furnished by the thorax and abdomen, has been discussed.

IV. THE THORAX

A. GENERAL.

The thorax of male coccids resembles the typical homopteran thorax much more than the coccid head resembles the typical homopteran head. The most striking feature of the thorax is the replacement of the hind wings by halteres and the resultant reduction of the metathorax. Sclerite degeneration is also very prevalent in some species and in some cases secondary ridges have been developed for reinforcing the thorax.

Many authors have in the past attempted the description of the thorax of male coccids, but these descriptions are usually incomplete and inaccurate and the parts are often not correctly identified. All these descriptions also suffer from the very serious disadvantage that it is only tergal and sternal structures that are always described and figured, while the pleural region is completely neglected. Mäkel's (1942) paper is almost the only publication in which pleural structures receive adequate attention. The reason for this neglect of the pleural region is probably due to the difficulty of making good slides of the insect in lateral view.

B. *MARGARODES VITIUM*.

Although the thorax of *Margarodes* is relatively large and all its component parts are easily visible, it has never been studied in any detail. The papers by Morrison (1928), Jakubski (1929) and Jancke (1955) contribute very little to our knowledge of the thoracic structures of this genus. Compared with other male coccids, the thorax of *Margarodes* is well sclerotized and distinctly divided into a pro-, meso- and metathorax.

(i) *Prothorax*.

The prothorax is not heavily sclerotized and, as in *Aphis* (Weber, 1928), a distinct neck membrane can only be distinguished dorsally. Laterally and ventrally the neck membrane is continuous with the membranous areas of the prothorax. Anterodorsally the prothorax has two sclerotized prominences which obviously represent the pronotum (prn) which has become discontinuous medially (Fig. 1). Three muscles are attached to the anterior margin of the pronotum (Fig. 4); two of these (9, 10) extend posteriorly to the mesoprephragma and the posttergite (pt) respectively, while the third one (8) goes ventrally to the tentorial bridge (tb). These muscles agree well with similar muscles attached to the pronotum in *Aphis* and aleyrodids (Weber, 1928, 1935a). The pronotum of *Margarodes* is however much less developed than in *Aphis* and aleyrodids and is widely separated from the pleural region.

Another broad, sclerotized area (pt.), surrounding a thick ridge is found dorsally on each side between the pronotum and the mesothorax. The anterior portion of this sclerite, as well as the ridge, terminates in a deep fold which almost resembles an invagination. This sclerite is very similar to and probably homologous with a sclerite which Weber in 1928 described as the posttergite in *Aphis*. In the figures appearing in his later works (1933, 1935b) he labels this sclerite the postnotum, but it is probably better to retain the name posttergite. It should, however, be made clear that the posttergite is probably merely a topographical term for a discrete posterior part of the pronotum and it is not homologous with the morphological unit which Snodgrass calls the posttergite in his textbook (1935). Muscles extending to the pronotum, cervical sclerite, ventral plate, coxa and mesoprephragma are attached to the posttergite.

The prothoracic pleural region is largely membranous and much flattened dorsoventrally (Fig. 3). It is produced laterally into a flattened lobular extension whose ventral surface is partially sclerotized to form a pleuron (pl). The pleural apophysis (pla) is invaginated from the ventral margin of this pleural sclerite and extends internally to quite near the anterior extremity of the posttergite. The pleural suture, with a strong internal ridge (plr), is very short and extends from the pleural apophysis to the base of the coxa, articulating with a dorsal process of the latter. As the pleural ridge does not extend dorsally beyond the apophysis, as it does in *Aphis* and *Psylla* (Weber, 1928, 1929), the pleuron is not completely divided into an anterior episternum and a posterior epimeron. The pleuron always has a narrow postero-ventral extension, but is not connected to the pronotum, as is found in other Sternorrhyncha. As in aleyrodids (Weber, 1935a), a trochantin is absent and the coxa therefore only has a dorsal, pleural articulation.

A very strong ridge (cv) also stretches anteriorly from the pleural apophysis and articulates with the posterior edge of the ocular sclerite (Figs. 2, 3). Although this ridge is intimately connected with the pleural ridge, its posterior margin can still be distinguished and doubtless represents a lateral cervical sclerite or laterocervicale, as is found in aleyrodids (Weber, 1935). According to Weber (1928, 1929) the cervical sclerite is incorporated in the episternum in *Aphis* and *Psylla* and conditions in *Margarodes* is also very reminiscent of those found in *Panorpa* (Snodgrass, 1935). Anteriorly the cervical sclerite has weakly sclerotized cuticle on both sides.

The whole of the ventral area between the coxae is membranous (Fig. 2) and the sclerotized prosternum (stn₁) is reduced to a very small triangular plate with a small internal apodeme representing a vestigial furca. This reduction in the extent of the sclerotized prosternum is also visible in *Aphis* and aleyrodids (Weber 1928, 1935a), but it has gone much further in *Margarodes*.

(ii) *Mesothorax*.

As the strong flight muscles are situated within the mesothorax, it is well sclerotized, especially dorsally where the mesotergum is distinctly divided into a notum or alinotum and a postnotum. The mesonotum is a strongly arched sclerite, and as in all other Pterygota, it is divided into three consecutive regions, the prescutum, scutum and scutellum by sutures which are actually lines of cuticular inflection forming internal ridges (Fig. 1).

The prescutum (prsc) is the most anterior part of the mesonotum and is separated from the scutum by two prescutal ridges (pscr) which are closely approximated medially. Externally these ridges form the prescutal suture (pscs). The anterior edge of the prescutum is continuous with that region which is folded in deeply to form the mesoprephragma (Fig. 5, phr₁), which is not bilobed, at the base of the fold. The strong median dorsal wing depressor muscles are not only attached to the mesoprephragma, but also to the prescutum which is strengthened for this purpose by the prescutal ridges. Each prescutal ridge is anteriorly fused with the mesoprephragma and at the point of fusion the notum is laterally produced into a prealare (pra) that extends ventrally to the episternum, with which it articulates. The prealare is pointed distally and both its anterior and posterior edges are folded sharply inwards, the anterior edge being continuous with the mesoprephragma.

The scutum (sct) is separated from the prescutum by the prescutal suture, which coincides with the internal prescutal ridges, and also laterally by a narrow strip of less sclerotized, more transparent cuticle. Posteriorly it is separated from the scutellum by the typically V-shaped scutoscutellar suture (scts). The lateral margin of the scutum is produced into an anterior notal wing process, but as in aleyrodids (Weber, 1935a) the posterior notal wing process and the lateral emargination are not distinct.

The scutoscutellar suture also forms an internal ridge which is interrupted medially, and which posteriorly runs through a rounded indentation on the surface of the notum. The scutellum (scl) is triangular in shape and its posterior margin is formed by another ridge which probably corresponds to the posterior marginal fold of the alinotum (scutellum) (rd) of Snodgrass (1935). This ridge and the scutoscutellar ridge coalesce laterally, forming

a sclerotized process which is connected ventrally to the postalare by means of a cuticular band. Similar conditions are found in *Aphis* (Weber, 1928).

The scutellum is followed posteriorly by the postnotum (pn), a broad triangular membranous area separating the two sclerites. A lateral prolongation of the postnotum, the postalare (pa) or lateropostnotum, extends anteroventrally to the pleuron where it pivots on the pleural ridge (plr) near the pleural apophysis (Fig. 3). In *Aphis* (Weber, 1928) the postalare is also movably connected to the pleuron, but in *Psylla* and aleyrodids (Weber, 1929, 1935a) it is immovably fused to the epimeron. The posterior portion of the postnotum extends very far back, but as it has been telescoped into the metathorax, most of it is invisible externally as it is overlapped by the metathorax and perhaps even part of the first abdominal segment. The wall of the postnotum appears to be double, but the hindmost wall is actually the metanotum (mtn) and the narrow mesopostphragma (phr₂), which is not emarginate medially, is formed ventrally where these two walls meet (Fig. 5). As in the case of the mesoprephragma, the strong wing depressor muscles are not confined to the phragma, but are also attached to the postnotum itself.

Apart from the phragma, the postnotum also bears two lateral, finger-like apophyses (pna), which are invaginated from its ventral edge at the points where the overlapping of the postnotum by the metathorax commences dorsally (Figs. 1, 5). These postnotal apophyses perhaps represent the anterior margin of an originally more extensive mesopostphragma and are probably homologous with the small V-shaped projections of the postnotum, which Weber (1935a) describes in aleyrodids. According to Larsén (1945) the mesopostphragma of *Ranatra* (Heteroptera) also has lateral extensions which are very similar to the postnotal apophyses of male coccids.

Because of sclerite degeneration and the development of secondary ridges, the structure of the pleuron is not quite as typical as that of the notum (Fig. 3) but the pleural suture, with a strong internal pleural ridge (plr), is quite distinct. Ventrally the pleural ridge forms a process for articulation with the coxa and dorsally it gives rise to a well developed pleural wing process (pwp). The pleural ridge does, however, not extend to the dorsal extremity of the pleural wing process. Between these two articulations the pleural apophysis (pla) is invaginated from the pleural ridge. The latter is not a true invagination but rather a gentle inward curving of the pleural ridge.

An episternum (eps) is found anterior to the pleural suture and is well sclerotized dorsally — where it forms a rounded prominence — but is replaced by membrane posteroventrally. As in *Aphis* (Weber, 1928) a long narrow membranous cleft separates the dorsal part of the episternum from the pleural wing process. According to Weber a small part of the episternum, which he calls the postepisternum, is also situated behind this cleft in *Aphis*. He then calls the large area in front of the cleft the preepisternum. In *Margarodes* there is however no indication that the whole of the sclerotized area behind the cleft is not the pleural wing process and the subdivision of the episternum into a pre- and postepisternum is therefore unnecessary. As in *Aphis* the ventral part of the episternum is distinctly separated from the remainder by a weakly sclerotized secondary ridge, not quite reaching the anterior margin of the episternum. For descriptive purposes this ridge will

be called the subepisternal ridge (ser). The triangular sclerite which is enclosed between the subepisternal ridge (a groove in *Aphis*) and another secondary ridge forming the lateral margin of the mesosternum, is called a lateropleurite (lpl) by Weber in *Aphis*, and he regards it as part of the episternum. This term will be retained in *Margarodes*, but it can probably equally well be regarded as a katepisternum. Roberti (1946) wrongly calls it a laterosternite in *Aphis*, as will be discussed lateron.

The prealare is supported by the episternum and is separated from it by a narrow strip of membrane (syndesis). Posterior to the prealare a well developed basalare (ba) is present. It is also separated from the dorsal margin of the episternum by membrane and articulates with the pleural wing process. Anteriorly it has a large dorsal extension which constitutes the lateral wall of a protuberance which bears the tegula dorsally (teg). The area behind the pleural suture is hardly sclerotized but a triangular, convex subalare (sa) whose anterior tip almost touches the pleural wing process, is present. The small sclerotized area immediately above the coxal articulation is all that remains of the epimeron (epm).

The mesothoracic spiracle (sp) is situated in the membrane anterior to the ventral part of the episternum. It is supported by a well developed peritreme (ptr) bearing an internal ridge.

The mesosternum (Fig. 2) has the appearance of a large, well-sclerotized, convex plate, which is fused laterally with the pleura in front of the coxae; precoxal bridges are therefore present, but postcoxal bridges are absent. The sternum is separated from the pleuron by a strong ridge which is also found in *Aphis* and *Psylla* (Weber, 1928, 1929) and which is fused posteriorly to the pleural ridge dorsal to the coxal articulation. Roberti (1946) describes this ridge in *Aphis frangulae*, calling it the laterosternal ridge on the assumption that the sclerotized area dorsal to it represents a laterosternite. Weber (1928) has shown, however, that in apterous aphids a laterosternite is present *below* this ridge which he calls the "Grenzleiste" or marginal ridge. As stated previously he regards the sclerotized area dorsal to the marginal ridge as part of the episternum and calls it the lateropleurite. The sternopleural region of *Margarodes* is very similar to that of *Aphis* and Weber's nomenclature for these parts will be used because it is probably more correct. The ridge separating the lateropleurite from the basisternum (laterosternite) will therefore be called the marginal ridge (mr) of the mesosternum.

Posterolaterally the mesosternum has two large semi-circular cavities or incisions covered by membrane, to which the coxae are attached. The coxae therefore have no sternal articulation. A strong ridge originating in the marginal ridge and ending medially in the vicinity of the mesofurca, runs along the edge of each of these coxal cavities and is joined anteriorly by the subepisternal ridge; an X-shaped structure is thus produced. Roberti (1946) describes an identical ridge in *Aphis* as the precoxal ridge (pcr), a term which will also be used in *Margarodes*.

The mesofurca (f) is very well developed and originates medially in a deep groove on the posterior margin of the mesosternum, thus indicating that the sternal plate of *Margarodes* is actually a basisternum (Fig. 5). The

furca is the only remaining part of the sternum and consists of a broad median portion bearing two furcal arms. The groove in which the furcal pit is situated, separates the mesosternum from the metasternum.

(iii) *Articulation of the Wings.*

The articulation of the wings is fairly typical of the articulation of the forewings in other Homoptera. Anterior to the wingbase a rounded, largely membranous protuberance is found, bearing a small meniscate sclerite dorsally. This sclerite is obviously the tegula (teg), as a muscle extending posteriorly to the anterior margin of the pleural wing process is attached to it. According to Weber (1933) this muscle is a very good criterion for the presence of a tegula. The muscle is attached to the pleural wing process by means of a tendon-like apodeme(t) which is not destroyed by KOH and is therefore still visible in cleared preparations.

The following pteralia take part in the articulation of the wings (Fig. 1):

- (a) the first axillary sclerite (1ax) is more or less triangular and its anterior tip, which is supported by the anterior notal wing process, curves round the tip of the second axillary sclerite and articulates with the costal complex of wing veins. Posteriorly it articulates with the lateral margin of the scutum.
- (b) The second axillary sclerite (2ax) is also triangular in shape and articulates anteriorly with the first- and posteriorly with the third axillary sclerite. Its ventral surface rests on the pleural wing process.
- (c) The third axillary sclerite (3ax) articulates anteriorly with the second axillary sclerite and posteriorly gives rise to a heavily sclerotized extension which apparently represents the axillary cord which has become fused to the third axillary. The axillary cord (axc) is connected to the postalare a short distance anterior to the point where the sclerotized band from the scutellum is attached, and the posterior marginal fold of the notum is therefore not directly connected to the wing membrane or axillary cord. It seems as if either the wing margin or the ridge formed by the posterior marginal fold of the notum has coalesced with the postalare for a short distance.
- (d) Although a fourth axillary sclerite cannot be distinguished, a small additional, weakly sclerotized plate (asc) is found distal to the second and third axillary sclerites. This additional sclerite in the wing membrane resembles the so-called "Zusatzstück" which Weber (1929) describes in *Psylla*.

The other thoracic elements taking part in the articulation of the wing are the anterior notal wing process, the pleural wing process and the basalare and subalare. Their structure and relationships have already been discussed previously.

(iv) *Metathorax.*

Because of the loss of functional hind wings, the metathorax of *Margarodes* has become very much reduced. The metanotum (mntn) originates morphologically posterior to the mesopostphragma, but as it does not extend

dorsally and posteriorly beyond the metathoracic fold, which overlaps the mesopostnotum, it is not visible externally (Fig. 5). Dorsally there are two small suspensorial sclerites (ss), which are connected to the bases of the halteres by sclerotized tendons (Fig. 1, ht). They must also form part of the metanotum and two strong muscles are attached to each of them. One muscle extends ventrally to the metafurca, while the other muscle is attached to the vesigial metathoracic basisternum. Contraction of these muscles will obviously lift the halteres.

The halteres are broad and have a single blunt apical projection which Morrison (1928) regards as a seta. The basal part is sclerotized and is slightly reminiscent of a wing vein.

The only other parts of the metatergum which are visible dorsally, are two weakly sclerotized plates (pn₃) of irregular shape which are found in the membrane posterior to the metanotum. Although no trace of a phragma could be found, these sclerites apparently represent the metapostnotum since each of them has a lateral extension which stretches down to the pleural region and may correspond to the postalare.

The metapleuron (Fig. 3) has a distinct pleural suture and ridge which articulates ventrally with the coxa and gives rise dorsally to the pleural wing process (pwp), which itself articulates with the base of the haltere. The pleural apophysis is barely distinguishable. As in the mesothorax, the epimeron (epm) is poorly developed; in the vicinity of the pleural wing process there is a small area which may be regarded as such and ventrally a narrow sclerotized strip is also found postero-dorsal to the coxal articulation. The episternum (eps) on the other hand, is fairly well developed and is bounded anteroventrally by a ridge whose homology is uncertain, but which probably corresponds to the subepisternal ridge (ser) of the mesothorax. A lateropleurite is absent. The precoxal ridge (pcr) has disappeared ventral to the episternum and a short stump at the anteroventral corner of the episternum is all that remains of it. It is however continued ventrally beyond this point and the small sclerotized area in front of it probably represents a vestige of the basisternum. A marginal ridge of the metasternum is absent.

The two sternal apophyses (sta) which are found ventrally (Figs. 2 and 5) have not united to form a furca, but there is a distinct groove and a slight ridge between them, which is reminiscent of the sternocostal suture. The sclerotized area between and behind the apophyses obviously represents the sternellum.

The metathoracic spiracle (sp) is situated anterior to the episternum and has a well-marked peritreme (ptr) with an internal ridge.

(v) *Legs.*

As in the *Margarodes* species studied by Morrison (1928) and Jancke (1955) the front legs (Fig. 36) are stout and heavily sclerotized and the one-segmented tarsus (tar), which is very closely associated with the tibia (tib), bears a large simple claw (cl). The middle and hind legs are however normal and slender and bear curious three-pronged claws (Fig. 35). According to Morrison, similar trifurcate claws are found in other species of *Margarodes*. The trochanters (tr) are all one-segmented and the coxae articulate only with the pleural ridges.

C. *PSEUDASPIDOPROCTUS* (?) *FULLERI*.

(i) *Prothorax*.

The prothorax of *Pseudaspidoproctus* is even less sclerotized than that of *Margarodes* and is separated from the head by a fairly distinct cervical groove. The pronotum (prn) is represented only by two small, weakly sclerotized anterior plates (Fig. 6) and the posttergite (pt) is also less extensive than in *Margarodes*. A narrow ridge runs along the middle of the posttergite and its anterior tip does not project inwards.

Laterally the cervical sclerite (cv) is represented by a strong ridge which articulates anteriorly with the posterior projection (p) of the postocular sclerite and is connected posteriorly to the pleural ridge (plr) in the pleural apophysis (Fig. 8). As in *Margarodes* the boundary between the cervical sclerite or ridge and the pleural ridge is quite distinct. The pleural apophysis (pla) is well developed but has no sclerotized area dorsal to it, as *Margarodes* has. The pleural ridge articulates ventrally with the coxa but does not extend dorsally beyond the pleural apophysis.

The prosternum (stn₁), of *Pseudaspidoproctus* is better developed than that of *Margarodes* and consists of a long medial ridge with a sclerotized area and a shallow sternal apophysis (sta) on each side (Fig. 7). Posteriorly the ridge is connected to a narrow transverse sclerotized area. The latter probably represents a sternellum.

(ii) *Mesothorax*.

The mesothorax of *Pseudaspidoproctus* is fairly similar to that of *Margarodes*, but the sclerotized areas are reduced. This is particularly noticeable dorsally where the mesoscutum exhibits several membranous areas. The division of the mesonotum into a prescutum, scutum and scutellum is however quite clear (Fig. 6).

The prescutum differs from that of *Margarodes* in that the short prescutal ridges (pscr) arise so far laterally that they take no part in the actual separation of the prescutum from the scutum (Fig. 8). The posterior margin of the prescutum is in actual fact formed by a strip of less sclerotized, more transparent cuticle, which is medially connected to a ridge (Fig. 6). The prescutal ridges are also peculiar in that they are not vertical but horizontal. This leads to the formation of a cavity between them and the dorsal wall of the prescutum. Anteriorly the prescutal ridges are connected to the mesoprephragma, which is bilobed and has a median ridge. The prelares (pra) are attached laterally to the prescutum and are separated from it by ridges. Both the anterior and posterior edges of the prelares curve strongly inwards, producing a trough-shaped structure which articulates ventrally with the episternum.

In contrast to *Margarodes*, the scutum (sct) is interrupted antero-medially by a large oblong membranous area, which is separated anteriorly from the prescutum by a ridge. The anterior notal wing process (anp) of the scutum is well developed and a distinct posterior notal wing process (pnp) is also present but a lateral emargination cannot be distinguished.

The scutellum (scl) is separated from the scutum by a typically V-shaped scutoscuteellar ridge (scts) which extends anteriorly to the membranous area of the scutum. Posteriorly the scutellum is bounded by a ridge which may be regarded (as in *Margarodes*) as the posterior marginal fold of the notum (rd). The posterior angles of the triangular scutellum are occupied by two roughly circular membranous areas. Laterally the scutellum is connected to the postalare by a narrow sclerotized band which is not as heavily sclerotized as in *Margarodes*.

A large membranous area intervenes between the scutellum and the postnotum (pn₂) which is much smaller than in *Margarodes*. It is only slightly overlapped by the metathorax, but possesses two well-developed, pointed postnotal apophyses (pna) and a bilobed postphragma. Anteriorly it forms the postalare (pa), which is strengthened by a thick internal ridge and articulates ventro-laterally with the pleural ridge.

In the pleural region the pleural ridge (plr) is very well developed and has a deep pleural apophysis (pla) dorsal to the point where it articulates with the coxae (Fig. 8). Dorsally the pleural ridge gradually fades out and disappears into the pleural wing process (pwp). The region in front of the pleural suture, which represents the episternum (eps), is well sclerotized except for the small ventral membranous area. The dorsal portion of the episternum is not visible externally as it is covered by membrane and projects internally. A lateropleurite is definitely absent and only traces of the sub-episternal ridge (ser) are visible. The basalare (ba) is found in the membrane dorsal to the rounded prominence of the episternum and articulates with the pleural wing process. It lacks the dorsal extension which is found in *Margarodes*. The area behind the pleural ridge is not sclerotized except for the subalare (sa) which is situated dorsally behind the pleural wing process and a small sclerotized area dorsal to the coxal articulation, which represents the epimeron (epm).

The mesothoracic spiracle (sp) is situated in the membrane anterior to the episternum. Ventrally it has a large peritreme (ptr) which lacks an internal ridge.

The mesosternum (which is composed entirely of the basisternum) is relatively smaller than in *Margarodes* but is strongly sclerotized (Fig. 7). The marginal ridges (mr) are medially fused with one another and form the anterior margin of the mesosternum. Posteriorly the mesosternum is bounded by the precoxal ridges (pcr). They extend further medially than in *Margarodes*. The furca (f) is very well developed and a short median ridge extends anteriorly from the furcal pit. A median ridge also occurs in the sternum of *Aphis* (Weber, 1928).

(iii) *Articulation of the Wings.*

The small rounded tegula (teg) is situated on a membranous bulge in front of and relatively far from the wing base (Fig. 6). In cleared specimens the tendon-like apodeme of the tegular muscle is clearly visible on the anterior edge of the pleural wing process.

The structure and relationships of the pteralia taking part in the articulation of the wings, are very similar to those of *Margarodes* and will only be discussed where they differ. The costal complex of wing veins (ccx)

have two articular processes. The dorsal one articulates with the anterior notal wing process, and the ventral one with the pleural wing process. The first and second axillary sclerites are very similar to those of *Margarodes*. The third axillary sclerite (3ax) apparently has no axillary cord associated with it, but basally it has a ventral appendage which may represent a fused fourth axillary sclerite. It does not seem to articulate with the posterior notal wing process, but rather with the postalare which has a small projection for the attachment of the wing membrane. The additional sclerite (asc) in the wing membrane is well-marked and relatively large. The other thoracic structures taking part in the articulation of the wings have been discussed previously.

(iv) *Metathorax*.

The metanotum originates at the mesopostphragma and, as in *Margarodes*, is not visible externally. Two small sclerites (ss), which are attached to the bases of the halteres by means of sclerotized tendons (ht) are found dorsally (Fig. 6). The halteres are similar to those of *Margarodes* but have 3 or 4 setae at the apex instead of a single apical projection. Further back there are two fairly large sclerotized areas which represent the metapostnotum (pn₃) and probably also incorporate parts of the first abdominal tergum. Each of these sclerites anteriorly has a slight lateral extension corresponding to the postalare, and the small sclerites situated laterally and medially to them are probably vestiges of the first abdominal tergites.

In the pleural region the pleural ridge (plr) is well developed and articulates dorsally with the base of the haltere and ventrally with the coxa (Fig. 8). A fairly deep pleural apophysis is found between these two articulations. Vestiges of sclerotized areas anterior and posterior to the pleural suture represent the episternum and epimeron respectively. As in *Margarodes* only the ventral part of the precoxal ridge of the metathorax is developed and it is continued dorsally as the subepisternal ridge. Above the pleural apophysis the subepisternal ridge fuses with the pleural ridge, separating off the ventral part of the episternum whose position however indicates that it does not correspond to the lateropleurite. The basisternum has disappeared completely but the sternellum, with a sternal apophysis (sta) and median ridge, is found medially (Fig. 7).

The metathoracic spiracle with its ventral peritreme is situated anterior to the episternum.

(v) *Legs*.

The legs are all very similar to the middle and hind legs of *Margarodes*, but a minute additional basal tarsal segment (tar₁) can be distinguished (Fig. 37). This is in accordance with the findings of Morrison (1928) and Lobdell (1937), who state that two-segmented tarsi occur in the males of most *Margarodidae*. The tarsal claws are all simple.

D. *STEINGELIA GORODETSKIA*.

In *Steingelia* the sclerotized areas of the thorax are even more reduced than in *Pseudaspidopectus* and also shows a certain number of modifications. The thorax has never been described before.

(i) *Prothorax*.

As the cervical groove is very deep, the prothorax is very well separated from the head. It is largely membranous and a conspicuous feature is the dorsal transverse ridge which is connected to the anterior tips of the propleura + cervical sclerites by sclerotized bands (Figs. 9, 11). Medially this ridge has two lobular posterior extensions. The homology of this structure is problematic; its position suggests, however, that it may be a very modified pronotum or part of a pronotum, and it also shows agreement with the so-called pretergite which Taylor (1918) describes in *Cicada*. As it is not interrupted medially, it is unlikely that it represents an additional cervical sclerite and it will therefore be called the pronotal ridge (prnr). A posttergite is completely absent.

The propleuron is also much modified (Fig. 11). A pleural apophysis is completely absent and the cervical sclerite is so intimately connected with the pleuron that the small ventral process, articulating with the coxa, is the only part of the pleural ridge that can be distinguished with certainty. The propleuron + cervical sclerite (plcv) is quite broad dorsal to the coxal articulation but is anteriorly transformed into a narrow ridge with a curved tip which is connected to the sclerotized band from the pronotal ridge. Posteriorly the propleuron + cervical sclerite has a weakly sclerotized extension.

The prosternum (stn₁) consists of a simple elongate ventral plate stretching almost up to the mouth opening and lacking pleural apophyses (Fig. 10).

(ii) *Mesothorax*.

The mesothorax is distinctly divided into a prescutum, scutum and scutellum (Fig. 9). The prescutum (prsc) is rounded and is separated from the scutum by a distinct groove (prescutal suture) which laterally coincides with the internal prescutal ridges (pscr). The prescutal ridges are well developed and stretch obliquely inwards, fusing anteriorly with the mesoprephragma which is not bilobed and whose ventral edge curves slightly upwards. Laterally the prealare (pra), whose structure is rather peculiar, extends from the notum to the episternum. Attached to the anterior margin of the pre-alare is a short apodemelike structure (a), which is produced by the infolding of its anterior edge in one place. Its distal extremity is also modified into a much more sclerotized triangular plate (tp) articulating with the episternum (Fig. 11).

As in *Pseudaspidopectus* the scutum (set) has a large triangular median membranous area (Fig. 9). Laterally it is produced into the anterior notal wing process (anp) and posterior to this process is a small notch which coincides with a line extending to the anterior margin of the scutellum, from which the lateral part of the scutum slopes steeply downwards for a short distance. Laterally this part of the scutum forms the rounded lateral emargination which precedes the posterior notal wings process (pnp). The latter probably incorporates the lateral part of the posterior marginal fold of the notum and is connected to the postalare by a weakly sclerotized band.

The scutellum (scl) is a very specialized structure in *Steingelia*. A V-shaped scutoscuteellar suture is completely absent and the scutellum is modified into a cylindrical structure with a median foramen (scf) in the

ventral wall of the cylinder. Conditions in some species of *Eulecanium* indicate, as will be discussed later, that this tubular type of scutellum is formed by the extension and eventual fusion of the internal scutoscutellar ridge and the posterior marginal fold of the notum. The function of the scutellar foramen, representing an area where fusion of these ridges has not taken place, is perhaps mechanical as it increases the flexibility of the scutellum and probably the mobility of the wings. A tubular scutellum without a foramen would have been much more rigid.

The postnotum is separated from the scutellum by a very large membranous area and is not visible dorsally as it is covered by the overlapping metathorax. Laterally the two broad postalares (pa) are quite distinct and articulate with the pleural sutures. As in *Margarodes* and *Pseudaspidoproctus*, the postnotum gives rise to two long postnotal apophyses and posteriorly to the mesopostphragma.

The pleural ridge (plr) is very well developed, ending dorsally in a large pleural wing process (pwp) and ventrally in a broad, rather weakly sclerotized process which articulates with the coxa (Fig. 11). The pleural apophysis is represented by an indentation of the pleural ridge. The episternum (eps) is well developed dorsally, where it forms a well sclerotized rounded prominence, but ventrally it is largely replaced by membrane. Anteriorly the episternum is bounded by the subepisternal ridge (ser) which, unlike *Margarodes*, has become separated from the precoxal ridge. The small sclerotized area situated between this ridge and the marginal ridge of the mesosternum obviously represents the lateropleurite (lpl). The area behind the pleural ridge is completely unsclerotized but an epimeron is possibly incorporated in the broad coxal articulation of the pleural ridge. A well defined basalar (ba) which articulates with the pleural wing process and the episternum, is present. Behind the pleural wing process an equally well developed subalare (sa) is to be found in the membrane. The mesothoracic spiracle (sp) with its peritreme (ptr) is situated in the membrane anterior to the subepisternal ridge.

The mesosternal plate (stn₂) which actually represents a basisternum as it is situated anterior to the furcal pit (fp), is bounded posteriorly by the precoxal ridge (pcr), but anteriorly the marginal ridge does not reach the median line as it does in *Pseudaspidoproctus* (Fig. 10). Laterally the basisternum is weakly sclerotized but medially it is traversed by a strong ridge. A large furca (f) is present. A small sclerotized area (s) is found medial to the coxa on each side. The homology of these sclerites is unknown, but they may be the vestiges of a sternal articulation of the coxae such as is found in the mesothorax of *Psylla* (Weber, 1929).

(iii) *Articulation of the Wings.*

The articulation of the wings and the articular sclerites are very similar to that described in *Margarodes* and *Pseudaspidoproctus* (Fig. 9). The additional sclerite is poorly defined and the third axillary sclerite is bounded by a heavily sclerotized tendon-like structure which is probably homologous with the axillary cord. The tegula (teg) is very small and lies very far forward. The tendon-like apodeme (t), by means of which the tegular muscle is attached to the pleural wing process, is distinctly visible.

(iv) *Metathorax*.

The metascutum is not visible externally, but two small suspensorial sclerites (ss) on which the sclerotized tendons from the halteres are inserted, are well developed (Fig. 9). Each haltere is elongate and narrow with two long, slender hooked setae at its apex. The anterior edge of the haltere is heavily sclerotized and it also has a distinct basal articular process. A post-notum (pn₃) is present, but its lateral parts, which probably represent the postalares, are well sclerotized and separated from the dorsal parts.

Laterally a very well developed pleural suture is present, but the pleural apophysis is absent (Fig. 11). The pleural ridge is forked dorsally where it articulates with the haltere and ventrally it has an articulation with the coxa. An episternum is present anterior to the pleural ridge, and as in *Pseudaspido-proctus*, the subepisternal ridge dorsally fuses with the pleural ridge. The epimeron is represented by a narrow, well sclerotized area dorsal to the coxal articulation of the pleural ridge.

The ventral continuation of the subepisternal ridge, which must be regarded as the precoxal ridge, bears a sclerotized area ventrally which is probably a vestige of the basisternum. Two well developed sternal apophyses (sta) are found ventrally between the coxae; the sclerite, which is situated between them, represents the sternellum.

The metathoracic spiracle with its peritreme is situated in front of the episternum.

(v) *Legs*.

The legs are fairly elongate (Morrison, 1928) and the one-segmented tarsus bears a simple curved claw (Fig. 38).

E. *EULECANIUM TAXI*.

The thorax of various lecaniids have been described very briefly by Green (1904-09), Sulc (1932), Pesson (1941), Dürr (1954) and Jancke (1955).

(i) *Prothorax*.

The prothorax is relatively short and is well separated from the head by a deep cervical incision. Apart from a few ridge-like structures, it is completely unsclerotized.

Immediately posterior to the neck region, two collar-like ridges, which articulate with the cervical sclerites, are found (Figs. 12, 14). These ridges are similar to and very probably homologous with the pronotal ridge of *Steingelia*, the only difference being that they have become interrupted medially and are not fused to the cervical sclerites + pleura. They are called the protergites by Habib (1953). In the pleural region the pleural sclerites and the cervical sclerite are so intimately associated that they form a single ridge-like structure (plev) which articulates anteriorly with the pronotal ridge and the postocular ridge and posteriorly with the coxa (Fig. 14). According to a figure from a paper by Crampton (1926), the cervical sclerite is similarly fused with the pleuron in *Coccus*, but an episternum and epimeron can still

be distinguished. A separate pleural ridge can no longer be distinguished, but there is an indication of a very slight pleural apophysis (pla). The prosternum (stn₁) is reduced to a strong transverse internal ridge without sternal apophyses, but with an anterior triangular sclerotized area (Fig. 13). A linear basisternum and sternellum is figured by Crampton (1926) in *Coccus*.

(ii) *Mesothorax*.

The primary division of the mesotergum into a prescutum, scutum, scutellum and postnotum, is correctly described in *Pulvinaria* by Pesson (1941), *Lecanium* by Sulc (1932) and *Physokermes* by Jancke (1955), but they give no further details. In *Eulecanium* the prescutum (prsc) is very nearly square and is bounded laterally by the prescutal ridges (pscr) which stretch obliquely inwards and extend posteriorly for some distance beyond the hind margin of the prescutum (Fig. 12). A transverse ridge, fusing laterally with the prescutal ridges, forms the posterior margin of the prescutum and is externally visible as the transverse part of the prescutal suture. The prescutum is slightly more heavily sclerotized medially. Anteriorly the prescutal ridges fuse with the mesoprephragma which is not bilobed.

In this region the scutum gives rise laterally to the prealare (pra) whose heavily sclerotized anterior edge is folded inwards and is continuous with the mesoprephragma. As in *Steingelia* the prealare ends distally in a convex, heavily sclerotized triangular plate (tp), articulating with the episternum.

The two lateral parts of the scutum (sct) are separated from each other by a median membranous area which is partially bounded laterally by the prescutal ridges and anteriorly and posteriorly by the prescutal suture and the anterior margin of the scutellum respectively. The anterior notal wing process (anp) is short, and rounded and not very distinct. A lateral emargination and posterior notal wing process is absent.

The scutellum (scl) is well developed and is shaped like a flattened tube. It is called the apodema by Green (1904—09) and Putnam (1878) in *Lecanium* and *Pulvinaria innumerabilis* respectively. As in *Steingelia* the ventral wall of the tube is pierced by a scutellar foramen (scsf) which is wrongly called a membranous area in *Pulvinaria mesembryanthemi* by Pesson (1941). Conditions in a species closely related to *Eu. taxi* indicated how this tubular type of scutellum, with its ventral foramen, comes into being. In this species (*Eu. tiliae* L.) the scutellum has the appearance of a slightly rounded plate whose edges curve sharply inwards. In the tubular scutellum the curved anterior, posterior and lateral edges of such a plate have evidently fused ventrally and the scutellar foramen represents a median area in which fusion has not taken place, perhaps for the mechanical reasons mentioned in *Steingelia*. Because the ventral edges of the scutellum have fused with one another, the V-shaped scutoscutellar ridge and the so-called posterior marginal fold of the notum are both absent. As in *Margarodes* the scutellum is laterally connected to the postalare by means of a very narrow sclerotized band.

A very large membranous area separates the postnotum from the scutellum. The postnotum (pn₂), which is regarded as the scutellum by Putnam (1878) and Green (1904—09), is almost entirely overlapped by the metathorax and only a small portion of it is visible dorsally. Posteriorly the postnotum gives rise to the mesopostphragma and further anteriorly to

the postnotal apophyses (pna). The postalares are broad and articulate anteriorly with the mesopleural ridges.

The pleural ridge (plr) is broad and very heavily sclerotized above the pleural apophysis (plr) and gives rise dorsally to the pleural wing process (Fig. 14). Below the pleural apophysis it is much narrower and forms a process for the articulation of the coxa. The strongly convex sclerotized area anterior to the pleural ridge represents the episternum (eps) which is dorsally separated from the pleural ridge by a long narrow membranous area. Ventrally the episternum is also partially replaced by membrane. The anterior margin of the episternum is formed by the subepisternal ridge (ser) which is not fused to the marginal ridge (mr). Between these two ridges a small lateropleurite (lpl) is found. A small sclerotized area dorsal to the coxal articulation represents the epimeron (epm). A basalar is completely absent, but a small triangular subalare (sa) articulates dorsally with the pleural wing process.

The mesothoracic spiracle (sp), which is supported ventrally by the peritreme (ptr), is situated anterior to the episternum.

The mesosternum (stn₂), consisting only of the basisternum, is heavily sclerotized and is bounded anteriorly by the marginal ridges, which are medially fused (Fig. 13). The precoxal ridges (pcr) do not extend far medially and the furcal pit, from which the furca (f) originates, lies between them. As in *Steingelia*, the sternum is divided by a strong median internal ridge.

(iii) *Articulation of the Wings.*

The articulation of the wings differs very little from that of the other species already described. The tegula (teg) is very far removed from the wing base and the tegular muscle is attached to the pleural wing process by a thin tendon-like apodeme (t). The costal complex of veins (ccx) has a dorsal process articulating with the anterior notal wing process and a ventral process articulating with the pleural wing process. The relationships of the articular sclerites are clear from the figures and are similar to those of *Steingelia*.

(iv) *Metathorax.*

As halteres are completely absent in *Eu. taxi*, the metathorax is even more reduced than in other male coccids. The metanotum is not visible dorsally and the postnotum as well as the suspensorial sclerites of the halteres are absent. In the closely related *Eu. tiliae* L. on the other hand, where halteres are present, conditions are very similar to those in *Steingelia* and the suspensorial sclerites of the halteres, as well as a small postnotum, are present.

The pleuron of *Eu. taxi* is equally reduced. The pleural ridge (plr), articulating with the coxa, is very short but divides the pleuron into a small episternum and a narrow, posteriorly directed epimeron. There is no trace of a pleural apophysis. In *Eu. tiliae* L. on the contrary, the pleural ridge is well developed, articulates with the haltere and forms a weak pleural apophysis.

The metathoracic spiracle is situated in front of the episternum. Metasternal plates and apophyses are completely absent.

(v) The legs are normal and slender, with distinctly one-segmented tarsi, bearing simple curved claws (Fig. 39).

F. *PSEUDOCOCCUS CITRI*.

A detailed description of the thorax of *Pseudococcus* is given by Mäkel (1942) and to a lesser extent by Berlese (1893). The papers by Vaney and Conte (1908), Cottier (1936) and Jancke (1955) contain no significant information on the structure of the thorax.

(i) *Prothorax*.

The structure of the prothorax is very similar to that of *Eulecanium*. It is separated from the head by a deep cervical groove and two pronotal ridges (prnr), articulating with the propleura + cervical sclerites, are found anteriorly (Figs. 15, 17). Mäkel (1942) regards these pronotal ridges as cervical sclerites, but conditions in *Steingelia*, where they are continuous dorsally, indicate that they most probably represent part of the pronotum. Each of the pronotal ridges dorsolaterally bears a less sclerotized projection which somewhat resembles the dorsal lobes of the pronotal ridge in *Steingelia*. Further back two small weakly sclerotized plates (pt) are found which may be vestiges of the posttergites. They are not described by Mäkel.

The pleural region is almost identical with that of *Eulecanium*. The pleuron + cervical sclerite (plcv) has been reduced to a capitate ridge-like structure, which articulates anteriorly with the postocular ridge and posteriorly with the coxa (Fig. 17). Mäkel (1942) calls this structure the propleuron and states that a small first cervical sclerite is anteriorly separated from it. Careful examination has however convinced me that the anterior tip of the cervical sclerite + propleuron is in fact not, as it may seem at first sight, detached from the rest of the structure. A small pleural apophysis (pla) can be discerned dorsal to the coxal articulation.

A small prosternum (stn₁) is found ventrally (Fig. 16). It consists of a small median triangular sclerite which is bounded posteriorly by a fairly long transverse ridge. The prosternum is not correctly figured by Mäkel (1942) and she calls it the ventral sclerite.

(ii) *Mesothorax*.

The division of the mesonotum into a prescutum, scutum and scutellum is very distinct. The prescutum, (prsc) which is strongly arched, is bounded laterally by the prescutal ridges (pscr) and posteriorly by a slight groove which represents the median part of the prescutal suture (Fig. 15). The prescutal ridges are well developed and are anteriorly fused to the mesoprephragma, which is slightly emarginate medially.

According to Mäkel the prescutum gives rise laterally to the prealare (pra), but actually the prealare is a lateral extension of the scutum in *Pseudococcus*, as the prescutal ridges have shifted far medially. The prealare is separated from the scutum by a ridge which extends relatively far posteriorly. As in *Steingelia* and *Eulecanium*, the prealare terminates in a heavily sclerotized convex triangular plate (tp) whose posterior edge, which articulates with the episternum, curves inwards, forming a distinct apodeme at its base.

The scutum (sct) is very large and weakly sclerotized medially. Laterally it is produced into a very well developed anterior notal wing process (anp) which curves upwards. As in *Steingelia* the line along which the lateral part of the scutum is folded sharply downwards, is indicated by a small notch behind the anterior notal wing process. A distinct lateral emargination is present and it is followed by the posterior notal wing process (pnp) which incorporates the posterior marginal fold of the notum along its hind edge. A sclerotized band connects it to the postalare. The prescutum + scutum is called the pronotum by Berlese (1893).

The anterior and posterior edges of the scutellum (scl), which is called the mesonotum by Berlese (1893), curve inwards, thus giving rise to a semicylindrical structure which, as in *Steingelia*, does not reach the lateral margin of the notum.

A large membranous area intervenes between the scutellum and the posterior part of the postnotum (pn₂), which is called the metanotum or postscutellum by Berlese (1893). Posteroventrally the postnotum merges into the mesopostphragma and laterally it gives rise to the two postnotal apophyses (pna), which are described as the "corniculate apophyses of the metanotum" by Berlese. Anterolaterally the postnotum is produced into the postalares (pa) which articulate with the pleuron anterior to the pleural ridge. Mäkel (1942) did not recognize the postalares as such and her interpretation of these structures is therefore quite erroneous. In *Pseudococcus* the dorsal margin of the postalare is strengthened by a ridge. Mäkel found this ridge, but she states, quite wrongly that it is fused with the pleural ridge. The ventral edge of the postalare is also reinforced by a ridge. Mäkel wrongly describes this ridge as originating at the pleural ridge and extending posteriorly until it meets the metathoracic pleural wing process.

The pleural ridge (plr) articulates ventrally with the coxa and terminates dorsally in the pleural wing process (pwp); in between is found a fairly deep pleural apophysis (Fig. 17). The sclerotized area anterior to the pleural ridge represents the episternum (eps) whose dorsal part is separated from the ventral by a membranous area. The dorsal part of the episternum is convex and its posterior edge is not visible externally because it projects internally for quite a distance. Its antero-dorsal edge is covered by the triangular plate of the prealare. The subepisternal ridge (ser) forms the anterior margin of the episternum and is not fused with the marginal ridge of the mesosternum. Only traces of a lateropleurite (lpl) is present. Dorsally there is a distinct basalare (ba) which Mäkel failed to identify as such. It extends between the episternum and the pleural wing process. As in *Eulecanium* a small area dorsal to the coxal articulation represents the epimeron (epm). Dorsally a distinct subalare (sa) is present behind the pleural wing process. Mäkel found this sclerite but did not name it. In general her description of the pleural region in *Pseudococcus* is very vague and also, as was mentioned previously, incorrect in some respect.

The mesothoracic spiracle (sp) with its supporting peritreme, is situated in the membrane anterior to the episternum.

As in *Eulecanium* the marginal ridges (mr) of the mesosternum (basisternum) are fused medially and form the anterior margin of this sclerite (Fig. 16). Posteriorly the precoxal ridges (pcr) are also fused with one another and the furcal pit is situated medially behind them. According

to Mäkel the area in front of the basisternum is weakly sclerotized and she calls it a presternite. This area is however definitely membranous in all the specimens examined by me and it can therefore be assumed that a presternum is absent. The furca (f) is called the metasternal apophysis by Berlese (1893) and also wrongly regarded as such by Larsén (1945).

(iii) *Articulation of the Wings.*

The articular sclerites of the wing are all very similar to those already described in the other male coccids (Fig. 15). The third axillary (3ax) has two basal processes; the articular membrane of the wing is attached to the posterior one and the anterior one apparently articulates with the postalare.

Mäkel's description of the pteralia is reasonably accurate. It seems however as if she has mistaken the costal complex of veins (ccx) for the second axillary sclerite and regards the true second axillary (2ax) as being part of the third. She also mistakes the distal upturned part of the anterior notal wing process for part of the costal complex of veins. In the pleural region she failed to see the basalare (ba) and does not name the subalare (sa).

(iv) *Metathorax.*

The metanotum is small and not visible dorsally. The suspensorial sclerites (ss) of the halteres, which Mäkel failed to see, are distinct and attached to the basal articular process of the halteres by means of sclerotized tendons (Fig. 15). Each haltere bears a distal hooked seta. A narrow sclerotized area further back represents the postnotum (pn₃) which is not described by Mäkel.

The pleural ridge articulates with the coxa and the haltere, but lacks a distinct pleural apophysis. Anterior to it a sclerotized episternum is found from which a ridge, probably representing the precoxal ridge, extends ventrally. An epimeron is present behind the pleural ridge. The metathoracic spiracle is situated anterior to the episternum.

Ventrally there are no sternal sclerites or apophyses.

(v) *Legs.*

The legs are slender and a small triangular additional tarsal segment (tar₁) is ostensibly present (Fig. 40). A tibio-tarsal articulation is definitely present, but it is doubtful whether the distinct articulation between the tarsal segments, which Lobdell (1937) mentions, really exists.

G. *AULACASPIS PENTAGONA.*

The diaspid thorax has received the attention of quite a number of workers on this group, but none of their descriptions is very satisfactory. Stickney's paper (1934) gives many details of thoracic structures in *Parlatoria blanchardi*, but unfortunately a number of the sutures and sclerotized areas which he describes are quite different in *Aulacaspis* and the other male coccids studied; these differences are probably due to Stickney's inaccurate observations.

(i) *Prothorax*.

The prothorax of *Aulacaspis* is not distinctly separated from the head and is even more membranous than that of *Pseudococcus* as the pronotal ridges are absent. Two small, very weakly sclerotized areas are visible dorsally on each side, and they may perhaps be representative of the pronotum (prn) and posttergite (Fig. 18, pt).

The pleuron + cervical sclerite (plev), which Nel (1933) calls the trochanter in *Aonidiella*, and Stickney (1934) the pleural sclerite in *Parlatoria blanchardi*, is fairly broad but does not extend so far anteriorly as to articulate with the postocular ridge (Fig. 20). Posteriorly it has a process for articulation with the coxa, but a pleural apophysis is completely absent.

The prosternum (stn₁) consists of a narrow median ridge without an internal apophysis, which is joined posteriorly by a narrow transverse sclerotized strip (Fig. 19). It is called the linear sternite of the prosternum by Berlese (1896) and Nel (1933) in *Aspidiotus* and *Aonidiella* respectively, but Stickney only refers to it as a "sclerotic area" in *Parlatoria*. Van Dinter (1950) also mentions it in *Chionaspis salicis* and Geier (1949) describes it as a "chitinous crest" in *Epidiaspis leperii*.

(ii) *Mesothorax*.

The mesonotum is distinctly divided into a prescutum, scutum and scutellum (Fig. 18). The rounded prescutum (prsc), which Berlese (1896) refers to as a prominence of the mesothorax and Targioni-Tozzetti (1867) calls the annular apodeme, is well sclerotized and is bounded by the prescutal suture which laterally coincides with the prescutal ridges (pscr). The prescutal ridges are anteriorly joined to the mesoprephragma which is not bilobed. As in *Pseudococcus* the prealare (pra) arises laterally from the scutum and its distal extremity is differentiated into a convex, almost crescent-shaped sclerite (tp) articulating with the episternum. Its anterior edge also curves inwards without, however, forming a distinct apodeme-like structure.

When compared with conditions in *Aulacaspis*, Stickney's (1934) descriptions of the prescutal region in *Parlatoria* are, in some respects, difficult to follow. It is impossible to ascertain what he regards as the prescutum; the true prescutum is called the scutum by him. His so-called precosta is perhaps the mesoprephragma. The undetermined sclerotized area which he describes in this region, is probably the basal part of the prealare, whose distal triangular portion he however identified correctly.

The scutum (sct) is slightly less sclerotized than the prescutum and is laterally produced into the anterior notal wing process (anp). Behind this process is a small notch which, as in *Steingelia*, marks the end of a curved line along which the lateral part of the scutum is folded down sharply. A lateral emargination is almost non-existent. The posterior margin of the scutum is formed by the posterior marginal fold of the notum, which is also connected to the postalare. Suter (1932) correctly states that thin sclerotized bars connect the scutellum with the wing roots in *Lepidosaphes*.

As in *Steingelia* and *Eulecanium*, the scutellum (scl) is tubular and the ridges, normally bounding the scutellum, are therefore not visible as such.

Targioni-Tozzetti (1867) calls it the transverse apodeme of the metathorax. Nel (1933), following Berlese (1896), calls the scutellum the interscutellar band, while Green (1896-99) refers to it as the apodema. The scutellar foramen (scf) in the ventral wall of the scutellum is very distinct. Berlese (1896) calls it a foramen in *Aonidiella*, although he clearly had no notion of the tubular nature of the scutellum, but Stickney (1934), Balachowsky (1937) and Jancke (1955) call it a membranous area. Balachowsky further states that this area is internally prolonged into an apophysis on which mesothoracic muscles are inserted, and Jancke also expressed the opinion that muscles are attached to the membranous area in *Aspidiotus*. These statements are however without foundation, since muscle attachments to the meson of the scutellum are not only absent in male coccids, but generally in all *Pterygota*. Berlese's (1896) observation that the longitudinal dorsal muscles are interrupted at and attached to the scutellum in *Aspidiotus*, is also wrong. These muscles extend between the mesoprephragma and the mesopostphragma without interruption.

A large membranous area separates the scutellum medially from the postnotum (pn₂) which is to a large extent overlapped by the metathorax. Nel (1933) again follows Berlese (1896) in calling the postnotum the scutellum and the same nomenclature is also followed by Green 1896-99). Posteriorly the postnotum gives rise to the mesopostphragma, which is slightly emarginate medially and further anteriorly the postnotal apophyses (pna), which are called the "corniculate processes of the scutellum" by Berlese (1896), arise. The postalaris are well-developed and are very broad where they articulate with the pleural ridge. Stickney (1934) apparently did not realize that the postnotum is telescoped into the metathorax. He correctly identifies the antecostal suture which internally bears the mesopostphragma, but he calls the posterior wall of the postnotum the precosta and the metanotum the postcosta. The phragma which he figures in this region represents the postnotal apophysis.

In the pleural region conditions are very similar to those described in the other genera (Fig. 20). The pleural ridge (plr) extends between the large pleural wing process (pwp) and the coxal articulation, and also gives rise to a strong internal pleural apophysis (pla). The ventral articular process of the pleural ridge, articulating with the coxa, is apparently regarded as a lateral apophysis by Berlese (1896). The area anterior to the pleural ridge is well sclerotized, but a membranous strip divides it into a dorsal and ventral part. Dorsally the episternum (eps) is separated from the pleural wing process by a cleft, and its anterior margin is formed by the subepisternal ridge (ser) which is not fused with the marginal ridge of the mesosternum. A distinct basalare (ba) is present, articulating dorsally with the episternum and the pleural wing process. The area behind the pleural ridge is completely membranous and an epimeral sclerite is therefore absent. A small round subalare (sa) is, however, present dorsally behind the pleural wing process.

Stickney's (1934) information on pleural structures is obviously based on a study of the dorsum and venter alone, and it is therefore incomplete and inaccurate. His pleural wing acetabulum is perhaps the pleural wing process, but it is impossible to determine what parts he designates as the "pleural wing condyle" and "alar butress". He recognized the pleural

apophysis, calling it an apodeme, but his interpretation of other pleural structures is confused and probably wrong.

Ventrally a strongly sclerotized mesosternum (basisternum) (stn_2) with a weak median ridge is present (Fig. 19). It is anteriorly bounded by the strong, fused marginal ridges (mr) and posteriorly by the precoxal ridges (pcr) which have also fused medially. The furca (f), which is well developed, is invaginated medially behind the basisternum. Reali (1954) wrongly described the mesofurca as being fused with the pleural apophysis in *Diaspis*. The precoxal and postcoxal bridges which Stickney (1934) describes as being attached to the mesosternum, are in reality the subepisternal and precoxal ridges respectively.

The mesothoracic spiracle (sp) has a small ventral peritreme (ptr) and is situated ventrolaterally some distance anterior to the episternum.

(iii) *Articulation of the Wings.*

The articulation of the wings is very similar to that of the male coccids described previously. Anteriorly a small tegula (teg), which Stickney (1934) calls an undetermined sclerite in *Parlatoria*, is found dorsally on a large membranous bulge in the body wall (Fig. 18). The first axillary sclerite (1ax) is fairly large and triangular, with the apex of the triangle pointing downwards. An additional sclerite is present (asc) but very indistinct. There appears to be no axillary cord but the third axillary sclerite (3ax) possesses a small anterior process. The articular membrane of the wing extends between it and a small projection on the postalare.

Stickney (1934) gives a detailed description of the articulation of the wings in *Parlatoria*, but it differs so much from that of other male coccids that its accuracy is doubtful. His descriptions and figures are very difficult to interpret, but it seems as if his first axillary sclerite is actually the costal complex of wing veins. It is impossible to determine what structures he regards as the second and third axillary sclerites, but his fourth axillary sclerite is really the first axillary sclerite, and his axillary cord the third axillary sclerite. His description of the other structures taking part in the articulation of the wings, has already been discussed. Schmidt's (1885) theory on the mechanism of wing movement in *Aspidiotus* differs so radically from the accepted theory on wing movement in insects that it is probably wrong.

(iv) *Metathorax.*

The metathorax is poorly developed. The metanotum extends dorsally and anteriorly from the mesopostphragma but is not visible externally. Two very small suspensorial sclerites (ss) are present at the bases of the halteres (h). Each haltere bears a single hooked seta (Fig. 18). The sclerotized tendon between the base of the haltere and the suspensorial sclerite could not be seen very clearly, but must obviously be present. Two weakly sclerotized areas further back represent the metapostnotum.

The pleural ridge articulates dorsally with the haltere and ventrally with the coxa and is called the epimeron by Berlese (1896) and the pleural sclerite by Stickney (1934). The pleural apophysis is completely absent.

A narrow sclerotized strip, which dorsally represents the episternum, lies anterior to the pleural ridge and stretches very far ventrally (Fig. 20). Berlese (1896) calls it a transverse branch of the epimeron. Ventrally it probably incorporates vestiges of the basisternum. A small posterior projection of the pleural ridge represents the epimeron. A sternellum is completely absent.

The metathoracic spiracles are situated very far forward, just behind the middle coxae.

(v) *Legs.*

The legs are fairly stout and the tarsi one-segmented (Fig. 41). The constriction, which is found at the base of the tarsus, cannot be regarded as an additional tarsal segment. The tarsal claws are simple and straight.

H. *DIASPIDIOTUS BAVARICUS.*

The thorax of *Diaspidiotus* differs very little from that of *Aulacaspis*.

(i) *Prothorax.*

The prothorax is largely membranous and very indistinctly separated from the head (Fig. 24). Two strange ramified structures (prnr) are found anteriorly and are probably homologous with the pronotal ridges of *Eulecanium* and *Pseudococcus*, as each also articulates ventrally with the cervical sclerite + pleuron (Fig. 26). A small weakly sclerotized dorsal area further back probably represents the posttergite.

The pleuron + cervical sclerite (plcv) is very similar to that of *Aulacaspis*. It articulates with the coxa and the pronotal ridge but has no articulation with the postocular ridge. A pleural apophysis is also absent.

A median ridge-like structure (stn₁), with a small round posterior sclerotized area, is all that remains of the prosternum (Fig. 26). Internal apophyses are absent.

(ii) *Mesothorax.*

The division of the mesothorax into a prescutum, scutum and scutellum is quite clear (Fig. 24). The prescutal ridges (pscr), which bound the prescutum (prsc) laterally, are fairly broad and very oblique. Posteriorly there is a distinct, though very narrow, ridge between them. The prescutal ridges are anteriorly connected to the mesoprephragma which is deeply emarginated medially. The prealare (pra) arises laterally from the scutum and as usual terminates in a convex triangular plate (tp) articulating with the episternum. The anterior edge of the prealare curves inwards, giving rise to an apodeme-like projection.

The scutum is not heavily sclerotized medially. Laterally it forms an indistinct anterior notal wing process but a lateral emargination and posterior notal wing process are altogether absent. The notch marking the end of the curved line along which the postero-lateral part of the scutum is folded downwards, is however distinct. As usual the scutum is posteriorly connected

to the postalare by a sclerotized band which is probably an extension of the posterior marginal fold of the notum.

The scutellum is very similar to that of *Aulacaspis*, but the scutellar foramen is much smaller. It is separated medially from the postnotum by a large membranous area. The postnotum (pn₂) is only slightly overlapped by the metathorax and posteroventrally terminates in the mesopostphragma. Further anteriorly two well developed postnotal apophyses (pna) are found and the broad postalares, which are very similar to those of *Aulacaspis*, articulate anteroventrally with the pleural ridge.

The pleural ridge (plr) is quite straight (Fig. 27). Dorsally it forms a large pleural wing process and ventrally articulates with the coxa. The pleural apophysis is well developed. An episternum, very similar to that of *Aulacaspis*, is present, but as usual an epimeron is lacking altogether. The subepisternal ridge (ser) is distinct and not fused with the marginal ridge of the mesosternum. A basalare (ba) is present dorsally and articulates with the episternum but seems to be fused with the pleural wing process. A very small subalare (sa) is present posterodorsal to the pleural wing process.

The mesosternum (basisternum) is very similar to that of *Aulacaspis*, but the precoxal ridges (pcr) are apparently not fused medially where the furcal pit is found (Fig. 26). A strong median ridge is present which is anteriorly fused to the marginal ridges of the mesosternum. The mesothoracic spiracle (sp) which is situated anterodorsally in the membrane, bears a very small peritreme.

(iii) *Articulation of the Wings.*

The articulation of the wings is so similar to those of *Aulacaspis*, that further discussions is not necessary. An additional sclerite could however not be distinguished. A well developed tegula is present.

(iv) *Metathorax.*

The metanotum extends dorsally from the mesopostphragma, but is not very extensive and not visible externally. The small suspensorial sclerites at the base of the halteres, identical with those of *Aulacaspis*, could not be found. They are perhaps not sclerotized enough to be recognizable.

The pleural ridge (plr) articulates dorsally with the haltere and ventrally with the coxa (Fig. 27). No pleural apophysis could be found. A narrow sclerotized area in front of the pleural ridge represents the episternum. The latter extends ventromedially and, as in *Aulacaspis*, must incorporate vestiges of a basisternum (Fig. 26, stn₃). No distinct epimeron is present, but the pleural ridge has a posteriorly directed process dorsal to the coxal articulation. This may represent the epimeron. The metathoracic spiracle is situated anterior to the episternum.

(v) *Legs.*

The legs are very similar to those of *Aulacaspis*, but a small segment apparently intervenes between the tarsus and tibia (Fig. 42). It is however indistinct and not button- or disc-like as Lobdell (1937) and Jancke (1955) found in other diaspid. The claws are simple and curved.

I. DISCUSSION.

A study of the thorax in male coccids immediately reveals that it is far less specialized than the head. In general it conforms well to the structure of the homopteran thorax and to a generalized insect thorax. The thorax of *Margarodes* is undoubtedly the most primitive of all the genera studied, but when its structure is compared with that of other Homoptera, various specializations become apparent. However, few of these specializations have brought about such striking anatomical changes as those found in the head.

The most important and obvious of the thoracic specializations is the transformation of the hind wings into halteres and the consequent reduction of the metathorax. The degeneration of the hind wings is accompanied by the atrophy of most of the metathoracic flight muscles, so that only the dorsoventral muscles attached to the suspensorial sclerites of the halteres, remain. The loss of the elaborate flight musculature is in turn accompanied by the reduction in size of the metatergum and metapleura, though the loss of sclerotized areas in the metathorax is perhaps also partly due to the process of desclerotization which is so manifest in other parts of the thorax.

Another part of the thorax which is highly specialized in *Margarodes*, is the postnotum. It is infolded into the metathoracic cavity, drawing the metanotum along with it, so that the latter is not visible externally. This condition is found in all the male coccids studied. Another specialization is the presence of the postnotal apophyses which are also developed convergently in the highly specialized *Ranatra* (Heteroptera) (Larsén, 1945). The articulation of the postalare with the pleural region is a specialized condition which is also found in *Aphis* (Weber, 1928), but the large membranous area separating the scutellum dorsally from the postnotum, is apparently confined to male coccids.

In contrast to the mesopostnotum, the structure of the mesonotum of *Margarodes* is very primitive. Anteriorly a prescutal suture delimits the prescutum and posteriorly a very typical V-shaped scutoscuteellar suture delimits the scutellum. The only specialization in this region is the apparent discontinuity between the posterior marginal fold of the notum and the wing margin; the sclerotized band connecting the scutellum with the postalare is formed by the posterior marginal ridge of the notum and either this ridge or the wing membrane has become fused to the postalare for a short distance. In all male coccids the mesonotum is very loosely connected to the pleura and the postnotum. Anteriorly the prealares articulate with the episternum and posteriorly the mesoscutum is connected to the postalares only by means of a weak sclerotized band. The pteralia are like those found in other Hemiptera, except that the axillary cord or the posterior margin of the wing has become fused with the third axillary sclerite. The latter is much more closely associated with the postalare than with the scutum.

The structure of the mesopleuron of *Margarodes* is also fairly primitive and has a great resemblance to that of the Aphididae and even Cicadidae. Its only specialized feature is the reduction in size of the epimeron, but this is probably due to sclerite degeneration, which has also invaded the lower part of the episternum. Because the epimeron is not developed dorsally, the postalare articulates with the pleural suture.

The notum of the prothorax is specialized in *Margarodes* in that it is very reduced and does not meet the pleuron. The presence of a posttergite is a specialization which *Margarodes* shares with the Aphidoidea and some Psylloidea (Larsén, 1945). In the propleuron the intimate association between the cervical sclerite and the pleuron represents a very specialized condition which is, apart from the Aphidoidea and Psylloidea, apparently not found in other Hemiptera although it occurs in some other orders, e.g. the Hymenoptera and Mecoptera. Another specialization of the propleuron is the disappearance of the pleural suture dorsal to the pleural apophysis, so that the weakly sclerotized pleuron is not completely divided into an episternum and an epimeron.

The sternal region of the thorax of all male coccids is very reduced and the sternal plates show no sign of the primary segmentation. In *Margarodes* the prosternum is very specialized, not only because it is so small, but also because the furca has been reduced to a single short internal projection. The mesosternum of *Margarodes* is no more specialized than that of other Sternorrhyncha and, although a median ridge is absent, it must have been subject to some degree of cryptosterny (Weber, 1933), since the furcal arms are situated on a median pedestal. Cryptosterny is obviously absent in the metasternum since the sternal apophyses are widely separated there. The metasternum of *Margarodes* is more specialized than in *Aphis* in that the small vestige of the basisternum is not connected to the sternellum and a precoxal bridge is therefore absent.

The reduction of the pretarsus to a single claw-like structure, in the Coccoidea, is a specialized condition not found in other Sternorrhyncha.

Apart from the specializations which the thorax of a primitive member of the superfamily Coccoidea, like *Margarodes*, exhibits when compared with the rest of the order Hemiptera, further specializations have also occurred within the superfamily itself. As in the head, sclerite degeneration has been a very striking phenomenon, reaching a peak in the highly specialized species.

(i) *Prothorax*.

The pronotum is most primitive in *Margarodes*. It has almost disappeared in *Pseudaspidopectus* and in *Steingelia* it is transformed into a peculiar pronotal ridge. The latter structure is still more specialized in *Eulecanium*, *Pseudococcus*, and *Diaspidiotus*, where it has become discontinuous dorsomedially and its complete absence in *Aulacaspis* probably represents a further specialization. The posttergite, which is elongate and has a median internal ridge in *Margarodes* and *Pseudaspidopectus*, is reduced to a flat, rounded, weakly sclerotized plate in the other species.

The propleuron also shows varying degrees of specialization. In *Margarodes* a pleural sclerite is still present dorsal to the pleural apophysis, but in *Pseudaspidopectus* this sclerite is absent and the cervical sclerite or ridge also becomes more closely associated with the pleural ridge. Conditions in *Eulecanium* and *Pseudococcus* are still more specialized since the cervical sclerite and pleural ridge become indistinguishably fused. A weak pleural apophysis is retained in these two genera, but this is also lost in *Diaspidiotus* and *Aulacaspis*. Apart from the fact that the propleuron + cervical sclerites

are anteriorly fused with the pronotal ridge, conditions in *Steingelia* are fairly similar to those in the latter two genera.

The prosternum is a very variable structure in male coccids and apparently is most primitive in *Pseudaspidoproctus* where two shallow sternal apophyses are present. In *Margarodes* only a short median internal spine is present on the small triangular prosternum. The prosternum of *Pseudococcus* and *Eulecanium* consists mainly of a fairly long transverse ridge, but in *Aulacaspis* and *Diaspidiotus* this ridge is longitudinal and very similar to that found in *Pseudaspidoproctus*. At this stage it is impossible to say which of these conditions are the most primitive and there is a strong possibility that the ridges are all secondary structures. The prosternum of *Steingelia* is aberrant in that it lacks both a ridge and apophyses.

(ii) *Mesothorax*.

In *Margarodes*, *Pseudaspidoproctus* and even *Steingelia* the prescutal ridges originate laterally so that the prescutum occupies almost the whole of the anterior part of the mesonotum. In the more specialized genera on the other hand, there is a marked tendency for the prescutal ridges to shift medially so that in *Eulecanium*, *Pseudococcus*, *Aulacaspis* and *Diaspidiotus* the prescutum is situated medially and the prelares actually arise anteriorly from the scutum. In *Margarodes* the posterior ends of the prescutal ridges are closely approximated medially, so that they also bound the prescutum posteriorly and the prescutal suture coincides with the prescutal ridges. In the other genera, however, the prescutal ridges are fairly straight and the posterior margin of the prescutum is formed by the prescutal suture only, which can be a groove (*Pseudococcus* and *Aulacaspis*), or weakly sclerotized strip (*Pseudaspidoproctus*), or even ridge (*Eulecanium* and *Diaspidiotus*).

The distal part of the prelare is quite normal in *Margarodes* and *Pseudaspidoproctus*, but in all the other genera it is very specialized and is modified into a heavily sclerotized, convex, triangular plate which is syndetically connected to the episternum.

The scutum of *Margarodes* is heavily sclerotized throughout, but in the other genera sclerite degeneration in the scutum has caused the development of median membranous areas, which are particularly well marked in *Pseudaspidoproctus*, *Steingelia* and *Eulecanium*. In the other genera the median membranous areas are less distinct. In *Steingelia*, *Pseudococcus*, *Aulacaspis* and *Diaspidiotus* a small secondary notch has developed behind the anterior notal wing process, and the lateral part of the scutum slopes steeply down along a line extending from this notch to the anterior margin of the scutellum. This specialization in the scutum is probably due to the peculiarity of the scutellum found in these genera.

The scutellum is very primitive in *Margarodes* and *Pseudaspidoproctus*, but in *Steingelia*, *Eulecanium*, *Aulacaspis* and *Diaspidiotus* it is very specialized forming a tubular structure which is bordered laterally by the scutum. Phylogenetically this tubular scutellum is probably not very significant, as it is present in *Eu. taxi* but absent in the closely related *Eu. tiliae*, the scutellum of which resembles that of *Pseudococcus* and is more primitive. The postero-lateral part of the scutum usually looks like the lateral part of the tubular scutellum, especially as the fold extending laterally from the anterior margin

of the scutellum sometimes has the appearance of a ridge. In *Margarodes* it is however very clear that the scutellum is bordered by the scutoscuteellar ridge and the posterior marginal fold of the notum. These ridges broaden and become fused ventrally in the tubular type of scutellum and the latter can therefore not extend beyond the limits of these ridges. In all the species where the scutellum does not reach the lateral margin of the notum, the posterior marginal fold of the notum becomes secondarily incorporated in the posterior edge of the scutum, connecting the latter with the postalare.

In all the species studied the postnotum is surprisingly similar and the only difference is the extent to which it is overlapped by the metathorax. These differences have no morphological significance.

The pleural region also varies but little among the different species and therefore shows few specializations. The subepisternal ridge, which is so well developed in *Margarodes*, is absent in *Pseudaspidoproctus*, but is present in all the other species. In these species however, the subepisternal ridge has changed its direction and forms the anterior margin of the episternum. It has also become detached from the marginal ridge of the mesosternum. Apart from *Margarodes* a well developed latero-pleurite is only found in *Steingelia*. Traces of an epimeron is found in *Margarodes*, *Pseudaspidoproctus*, *Eulecanium* and *Pseudococcus*, and may also be present in *Steingelia*. Its absence in the diaspidids must be regarded as a specialization. The pleural region of *Eulecanium* is peculiar in that a basalare is completely absent.

The mesosternal plate of all male coccids represent a basisternum, as it is situated in front of the furcal pit. It shows very little variation, and the variation which is present, is of no morphological or phylogenetic importance. The marginal ridges of the mesosternum are fused medially with one another in all the species, except *Margarodes* and *Steingelia*. As was stated previously, the median ridge of the basisternum is secondarily absent in *Margarodes* and it is also absent in *Pseudococcus*. Traces of it are however present in *Pseudaspidoproctus* and in *Steingelia*, *Eulecanium*, *Aulacaspis* and *Diaspidiotus* it is very well developed but this should probably not be regarded as a primitive feature, as these species are so specialized in other ways. The small sclerites which are found near the coxae of *Steingelia*, are perhaps comparable to the sternal articulation of the coxa in *Psylla* and therefore represent a very specialized condition.

(iii) *Metathorax.*

The metathorax is a very specialized structure even in *Margarodes*. A metanotum is present in all species and the suspensorial sclerites of the halteres are only absent in *Eu. taxi*, which has also lost its halteres. The broadness of the halteres in *Margarodes* and *Pseudaspidoproctus* is a primitive characteristic. The postnotum is also fairly large in these two species, but could not be distinguished in *Diaspidiotus*. The small differences found in the pleural region are of no phylogenetic importance, but the presence of a sternellum and sternal apophyses in *Margarodes*, *Pseudaspidoproctus* and *Steingelia*, is definitely a primitive feature.

(iv) *Legs.*

The modified front legs of *Margarodes vitium* and probably also the trifurcate claws borne on the middle and hind legs, are obviously special adaptations to the fossorial habits of this species. The presence of a small additional basal tarsal segment in some Coccoidea, is apparently of no phylogenetic importance as its appearance is not constant even in closely related species (Lobdell, 1937). In the specimens examined by me, this additional tarsal segment was never very distinct, but the fact that it may be present is nevertheless of interest, since it was almost universally accepted in the past that the coccid tarsus is one-segmented.

In conclusion it may be said that two factors, namely the reduction of the hind wings and sclerite degeneration, are mainly responsible for the modifications and specializations in the thorax. In spite of this, the thorax is a fairly homogenous structure in all the male coccids studied and the number of identical specializations which are found, lead one to the same conclusion as the study of the head did, namely that the superfamily Coccoidea is a monophyletic group.

V. THE ABDOMEN

A. GENERAL.

Apart from the variations found in the genital segments, the structure of the abdomen of male coccids is fairly uniform. It has become largely membranous through sclerite degeneration and the segmental boundaries, as well as the dividing line between the abdomen and the metathorax, are seldom distinct in cleared preparations. The segmentation of the abdomen is therefore best studied by observing the segmental arrangement of the longitudinal abdominal muscles in longitudinal serial sections.

In all the species studied, the abdomen has eight pregenital segments, but the *first* abdominal segment is never developed ventrally. According to Stickney (1934), Snodgrass expressed the opinion privately to him that in coccids, "the metathoracic legs have crowded out in this region the first abdominal segment".

B. *MARGARODES VITIUM.*

The general structure of the abdomen of *Margarodes* has much in common with that of *Aphis*. Jakubski (1929) mentions that there are eight abdominal segments in *Margarodes polonicus*, but Jancke (1955) makes no definite statement about the number of abdominal segments in the various margarodid species which he describes. Eight pregenital segments can, however, be distinguished in *Margarodes vitium* (Fig. 28) and segments I—VII each bear a pair of spiracles (sp). The first abdominal segment is quite distinct dorsally as it bears a large tergal plate (at_1), which is well separated from the metapostnotum. As in *Aphis* (Weber, 1928), however, this segment cannot be distinguished ventrally since its sternal sclerotization has been obliterated. In segments II—VIII, on the other hand, the sternal plates (ast)

are quite large and form a median keel for the abdomen. The 8th sternite (ast_8) is considerably larger than the other abdominal sternites and is thickened dorsally, where it articulates posteriorly with the penial sheath.

In segments I—III the tergites (at_{1-3}) consist of large transverse plates, but in segments IV and V they are discontinuous medially and have also been subdivided into anterior and posterior parts. The tergal sclerotizations of segments VI and VII have been modified because of the presence dorsally in each of the two segments of a transverse band-like cluster of glands (gl), which surround long glassy threads and which were called tubular pores or ducts by Morrison (1928). In segment VI one short transverse sclerotized strip runs dorsally to the cluster of pores and another narrow elongate transverse sclerite, stretching far laterally, runs ventral to it. In segment VII there are similar but slightly broader and medially discontinuous sclerotized areas dorsal and ventral to the cluster of pores. The tergum of segment VIII consists of a pair of small oblong plates near the anterior margin of the segment.

As is the case in most other insects, the 9th abdominal segment is modified in connection with the presence of external genitalia. Compared with many other Homoptera, the external genitalia of *Margarodes* are simple and consist only of a median copulatory organ or penis, and a conical penial sheath which encloses the basal part of the penis. The penis (pen) is a simple tubular, heavily sclerotized, trumpet-shaped organ, not unlike that of aleyrodids (Weber, 1935a) or *Aphis* (Roberti, 1946), but less complicated than that of other Homoptera. It contains the ductus ejaculatorius, which apparently terminates in an eversible endophallus. The latter opens externally through an apical slit in the posterodorsal wall of the penis. The inner genital aperture or basal foramen of the penis is very large and its dorsal rim is curved upwards; its ventral rim is produced into a short lip which is connected to the ventral wall of the penial sheath and perhaps represents the basal plate prolongation, which Singh-Pruthi (1925) describes in Homoptera. The penis obviously pivots on this ventral lip and protrudes ventrally through the slit in the penial sheath when muscles, extending between the dorsal edge of the aperture and the dorsal wall of the 8th abdominal segment, contract.

The penial sheath (ps) is well sclerotized laterally, but dorsally it is largely membranous, except at its posterior tip. Ventrally the penial sheath is cleft by a long narrow slit, whose edges overlap slightly, and through which the penis protrudes (Fig. 31). The ventral lip of the penis is attached where this slit commences near the anterior margin of the penial sheath. The anterior edge of the penial sheath is heavily sclerotized laterally and is ventrally produced into a short internal projection (pr). When the genital segment of *Margarodes* is compared with that of other Homoptera, it is fairly obvious that the penial sheath represents the enlarged lateral parts of the 9th abdominal sternum, which have become fused posteriorly and which were called pygofer by Singh-Pruthi (1925) and Kershaw and Muir (1922).

Morrison's (1928) suggestion that the penial sheath represents fused 'gonapophyses' is somewhat unsatisfactory in view of the loose nature of this term. The fact that the anterior border of the sheath is in almost immediate contact with the 8th sternite makes it rather improbable that the whole sheath could represent the harpagones (claspers) or parameres (the two elements to which the name 'gonapophyses' has been applied). The two

most likely possibilities seem to be (a) the whole sheath represents a modified 9th sternum or (b) the sheath consists basally of the 9th sternum and apically of the harpagones and/or parameres. The incorporation of the harpagones is perhaps rather unlikely in view of Qadri's (1949) contention that they have disappeared in other Sternorrhyncha, where the aedeagus is a tripartite structure consisting of penis + parameres. It is, however, hardly possible to decide between the remaining alternatives, which are

- (a) Sheath composed entirely of 9th sternum; parameres absent, penis forms intromittent organ.
- (b) Sheath composed entirely of 9th sternum; parameres indistinguishably fused with penis.
- (c) Sheath formed from 9th sternum fused with parameres; penis forms intromittent organ.

On the whole, the last alternative is unlikely if the ventral lip of the penis really represents the basal plate prolongation and there is not really much difference between alternatives (a) and (b).

The anus is situated in the membranous area dorsal to the penial sheath and the small transverse sclerite, which is situated in front of it, is probably the 9th abdominal tergite. The tergites of the 10th and 11th abdominal segments, which occur in many other Homoptera, are not developed in *Margarodes*, but these segments may be incorporated in the membranous area surrounding the anus.

C. *PSEUDASPIDOPROCTUS* (?) *FULLERI*.

Compared with *Margarodes*, the abdomen of *Pseudaspidoproctus* is much more flattened dorsoventrally and the tergites (at) and sternites (ast) have been reduced in size and are subdivided into a number of small, narrow, elongate transverse plates (Figs. 6, 29, 30). Eight pregenital segments can be recognized (the 1st abdominal segment cannot be distinguished ventrally) and segments IV—VIII each bears a pair of abdominal spiracles. Segment VIII posteriorly bears two unsclerotized tubular appendages (cap), almost as long as the rest of the body, which probably represent caudal extensions of the lateral bulges found in the other pregenital segments (Figs. 29, 30). According to Morrison (1928) similar appendages of varying length are found in all monophlebid and Green (1924) states that there are four pairs of these appendages in *Monophlebus phillippensis*.

Both the tergal and the sternal plates are very narrow and are situated on the segmental boundaries, therefore in the antecostal region where the segmental muscles are attached. They may be regarded as belonging to the segments behind them. The tergites of the 1st abdominal segment are apparently fused with the metapostnotum, but those of the 2nd abdominal segment (at₂) consist of six small plates (Fig. 6). Those of the other segments are more elongate, especially the median pair, but in segment VIII only four tergites are developed (Fig. 29). Ventrally the 2nd abdominal segment bears 5 small sternites (ast₂), the most lateral of these lying very close to the metepimera (Figs. 7, 8). Further back these sternites increase in number to six or more, become linear and are not always well separated from one another. The median sternite of segment VIII has however been extended anteriorly and posteriorly to form a large ventral plate with a

strong internal ridge, probably representing the antecosta of this segment (Fig. 30).

In spite of the fact that *Margarodes* and *Pseudaspidopectus* are closely related, the shape of their genital organs is very different. Morrison (1928) gives only short descriptions of the genital segment in some monophlebid, but Singh-Pruthi (1925) describes its morphology in detail in *Monophlebus stebbingi* and Misra (1939) studied its development in *Drosichiella (Monophlebus) quadricaudata*.

The penis (pen) of *Pseudaspidopectus* consists of a wide, relatively short, straight tube, which does not narrow posteriorly (Figs. 29, 30). As in *Margarodes* the dorsal rim of the internal genital aperture curves upwards, and the ventral rim is connected to the ventral wall of the penial sheath where the median slit, through which the penis protrudes, originates anteriorly. An eversible endophallus can be recognized, but this is not very distinct.

The penial sheath (ps), which encloses the base of the penis, is much smaller than in *Margarodes*, and Singh-Pruthi (1925) calls it the "aedeagus basal support" in *Monophlebus*. He also states that parameres are absent and therefore obviously does not regard the penial sheath as consisting of fused parameres. Misra (1939) states that in *D. quadricaudata* the penial sheath is continuous with the 7th abdominal sternite, but this is not the case in *Pseudaspidopectus*, where it definitely occupies part of the region of the 9th abdominal segment.

The anus (an) is situated dorsal to the penial sheath between the caudal appendages. A sclerotized ring, which may represent the fused 9th tergite and 10th abdominal segment, surrounds the anus. Ventrally it is connected to the penial sheath by a narrow median sclerotized band.

D. *STEINGELIA* GORODETSKIA.

The abdomen of *Steingelia* is elongate and flattened dorsoventrally and consists of eight pregenital segments. It is largely membranous and apart from the 8th abdominal segment, where a pair of well sclerotized, transverse sternal plates (ast_8) is present (Fig. 32), the other tergites and sternites are only just visible as poorly defined, extremely weakly sclerotized transverse bands. The 8th abdominal segment dorsally bears two clusters of pores, each cluster surrounding 2 or 3 stout setae. Segments I—VI each bears a pair of spiracles.

The genitalia are briefly described and figured by Morrison (1928). The penis (pen) is long and curved and fairly similar to that of *Margarodes* (Fig. 32). Its internal aperture is large and the elongated ventral rim of this aperture is attached to the posterior edge of the ventral sclerotized band of the penial sheath.

The penial sheath (ps) is largely membranous but a narrow sclerotized band runs ventrally near its anterior margin and extends posteriorly along its sides. The bands of opposite sides fuse posteriorly at the sharply pointed apex of the penial sheath. The median slit, through which the penis protrudes, is quite short and does not extend anteriorly to the ventral rim of the internal genital aperture of the penis, as it does in *Margarodes* and *Pseudaspidopectus*. The area dorsal to the sclerotized band of the penial sheath is completely membranous and contains the anus. 9th and 10th abdominal tergites are not developed.

E. *EULECANIUM TAXI*.

Apart from the external genitalia, the abdomen of *Eu. taxi* is almost completely membranous. As in *Eu. tiliae* (Sulc, 1932), *Pulvinaria mesembryanthemi* (Pesson, 1941), *Pulvinaria innumerabilis* (Putnam, 1878) and the various lecaniid males described by Silvestri (1920), eight pregenital segments can be distinguished. The 8th segment bears two pointed lobe-like caudal extensions (ce) and medial to these lobes is a pair of funnel-shaped pits, from each of which two stout setae arise (Fig. 34).

No abdominal tergites could be distinguished, but a weakly sclerotized 7th sternite (ast₇) and a well sclerotized 8th sternite (ast₈), are present. The 8th sternite extends far laterally and, as in *Pulvinaria innumerabilis* (Putnam, 1878), surrounds the base of the penial sheath (ps), which has become very elongate to form a caudal stylus. The latter is well sclerotized laterally but is membranous dorsally and ventrally. The ductus ejaculatorius runs along the penial sheath for some distance and as in *Eu. tiliae* (Sulc, 1932), posteriorly gives rise to the penis (pen), which is very weakly sclerotized and difficult to distinguish. It protrudes through a ventral slit near the apex of the penial sheath.

The anus is situated in the dorsal membranous area at the base of the penial sheath. Sulc (1932) describes a 10th and 11th abdominal tergite in *Eu. tiliae*, but these sclerites could not be found in *Eu. taxi*; a 9th abdominal tergite is apparently also absent.

F. *PSEUDOCOCCUS CITRI*.

The abdomen of *Pseudococcus* is described in detail by Berlese (1893) and Mäkel (1942). Both these authors recognized the usual eight pregenital segments and regard the 9th as the genital segment.

The first two abdominal segments each bear two small indistinct tergites and the 8th abdominal segment bears a pair of small triangular sternites (ast₈) and a broad transverse tergal plate (Fig. 33). Apart from these sclerotizations, the pregenital segments of the abdomen are completely membranous. Two groups of long setae arise laterally near the posterior margin of the 8th abdominal segment.

Although the structure of the penis is rather peculiar, the external genitalia of *Pseudococcus*, which are described fairly well by Mäkel (1942) and Berlese (1893), are more similar to those of *Margarodes* than those of *Eulecanium*. The penis (pen) consists of a wide dorsal tube which narrows abruptly posteriorly and then opens at the flattened tip of a curved, heavily sclerotized bar, which runs along the ventral wall of the tube. This bar extends anteriorly to the internal genital aperture (iga) and is then continued as a short basal rod (bra) which eventually fuses medially with the ventral wall of the penial sheath. When compared with the penis of *Margarodes*, it is clear that in *Pseudococcus* the ventral wall of the penis has become more heavily sclerotized and the ventral lip of the internal genital aperture has been lengthened to form the basal rod connecting the penis with the ventral wall of the penial sheath.

The penial sheath (ps), which is called the genital valve by Berlese (1893), is more sclerotized than in *Steingelia*. It terminates posteriorly in a

short, slightly curved projection and ventrally bears a small heavily sclerotized lobular extension on each side. The latter structures perhaps function as claspers during copulation, and between them is a small membranous area containing the ventral slit through which the penis protrudes. This slit runs anteriorly up to the point where the basal rod of the penis is fused to the narrow sclerotized anteroventral wall of the penial sheath. The anterior edge of the penial sheath is very heavily sclerotized, forming two broad, ridge-like structures which are not fused with one another ventromedially.

The anus is situated in the membrane dorsal to the penial sheath. The small sclerotized area dorsal to the anus probably represents the fused 9th tergite and 10th segment.

G. *AULACASPIS PENTAGONA*.

The abdomen of *Aulacaspis* is flattened dorsoventrally and the abdominal segments gradually become narrower posteriorly. Eight pregenital segments can be distinguished, the first abdominal segment not being developed ventrally. The external genitalia are situated in the 9th abdominal segment. The same number and arrangement of the abdominal segments are described in various Diaspididae by Witlaczil (1886), Berlese (1896), Green (1896—99), Stickney (1934) and Geier (1949). Nel (1933) and van Dinther (1950), on the other hand, state that there are only eight abdominal segments in *Aonidiella* and *Chionaspis salicis* respectively. In view of conditions in all the male coccids studied, the accuracy of this observation is doubtful. The 8th abdominal segment of *Aulacaspis* bears a pair of weakly sclerotized tergal plates (at_s) which is situated very far laterally (Fig. 25); these are the only sclerotized areas in the pregenital segments.

The external genitalia consist of a penis (pen) and penial sheath (ps) and are fairly accurately described by most authors although few of them give details. The penis is heavily sclerotized but thin and very elongate, extending posteriorly for almost the whole length of the stylus of the penial sheath. As in *Pseudococcus* a long, median heavily sclerotized basal rod (bra) extends from the internal genital aperture (iga) of the penis to the ventral wall of the penial sheath. A similar rod is described in *Lepidosaphes ulmi* by Suter (1932) and van Dinther (1950) also mentions a similar structure in *Chionaspis salicis*.

The penial sheath (ps) is very well sclerotized and consists of a rounded basal part, which is posteriorly produced into a very elongate stylus (st). The lateral parts of the base of the sheath are fused dorsally with each other anterior to the small membranous area which surrounds the anus. A strong internal ridge forms the anterior margin of the penial sheath; it is however not developed dorsally. Ventrally at the point where the basal rod of the penis is attached to the floor of the penial sheath, a slit, comparable to that of the other male coccids studied, originates and stretches posteriorly for the whole length of the stylus. Where the stylus originates dorsally, the edges of the ventral slit are thickened and produced internally into two anteriorly directed processes (pro). The stylus is well sclerotized dorsally.

The small dorsal rounded membranous area, surrounding the anus, is probably a vestige of the 9th and 10th abdominal segments. A sclerotized 10th tergite is absent.

H. *DIASPIDIOTUS BAVARICUS*.

The abdomen of *Diaspidiotus* is very similar to that of *Aulacaspis*. It also consists of 8 pregenital segments, but the tergites of the 8th abdominal segment are not developed.

All that has been said about the external genitalia of *Aulacaspis*, applies equally well to *Diaspidiotus* and the description and figuring of the genital segment of the latter is therefore superfluous.

I. DISCUSSION.

Sclerite degeneration is very pronounced in the abdomen of most male coccids and has secondarily caused the reduction of most of the visceral sclerotized areas. In this respect *Margarodes* is primitive as it has retained well developed tergal and sternal plates and the desclerotization of its abdomen has proceeded no further than in other Sternorrhyncha. The elimination of the sternal region of the first abdominal segment is a specialization which, among the Sternorrhyncha, the Coccoidea share with the Aphidoidea.

In male coccids the external genitalia are not very complex, mainly because of the absence of the various periphallallic structures, which are generally found in Homoptera. The relative simplicity of the external genitalia is, however, not a primitive condition (a view already expressed by Qadri, 1949) and the harpagones and other accessory periphallallic structures have probably been lost secondarily. Singh-Pruthi (1925) apparently regards the form of the penis and the absence of parameres and subgenital plates as primitive features in the Coccoidea, but the absence of basal plates as a specialization. In *Margarodes* the genital segment is probably the most primitive, but in the more specialized species, the 9th abdominal segment has undergone various modifications. An important specialization is the caudal prolongation of the penial sheath and penis in *Eulecanium* and *Diaspididae*. In these insects the development of a "scale" in the female is obviously correlated with the formation of a long copulatory stylus, which can be inserted underneath the scale during copulation.

With the exception of *Eulecanium*, the penis is connected medially to the ventral wall of the penial sheath in all the species studied. In *Margarodes* and *Pseudaspidopectus* this connection is very short, but in the more specialized species it is long and rod-like, reaching its greatest length in the Diaspididae. It is very probable that this connection between the penis and the penial sheath, which may incorporate the basal plates of the penis, represents the fused "basal plates prolongation" or "lateral processes of the basal plates", which Singh-Pruthi (1925) and Marks (1951) respectively described in the Homoptera. According to Marks (1951) the lateral processes of the basal plates are greatly elongated but paired in *Pachypsylla*. In aleyrodids, however, Weber (1935a) describes a long unpaired ventromedial projection of the penis, which has a great resemblance to the basal rod of the penis in coccids.

The degree of sclerotization of the penial sheath varies considerably in different species, but is probably of no phylogenetic importance. The fusion of the lateral parts of the penial sheath anterior to the anal opening, in

Aulacaspis and *Diaspidiotus*, is however a specialized condition which was not found in the other species.

The retention of abdominal spiracles in *Margarodes*, *Pseudaspidopectus* and *Steingelia* is obviously a primitive feature and their loss in the other species a specialization.

VI. GENERAL DISCUSSION AND CONCLUSIONS.

This study of the morphology of male coccids has brought to light a considerable number of new facts concerning

- (a) the phylogenetic relationship of the Coccoidea with other Sternorrhyncha and
- (b) the affinities of the various subdivisions of the superfamily Coccoidea itself.

A. RELATIONSHIP OF COCCOIDEA WITH OTHER STERNORRHYNCHA.

A number of authors have in the past commented on the affinities of the Coccoidea within the series Sternorrhyncha. Few of them, however, give reasons for allocating certain positions to the Coccoidea in their phylogenetic trees, and, since very little information on the anatomy of the males was available, it must be assumed that their suggestions are on the whole only tentative and based largely on the phylogenetically unreliable evidence supplied by the anatomy of the neotenic females.

Osborn (1895) was one of the earliest authors to realize that the Coccoidea are a highly specialized group; prior to the publication of his paper the Coccoidea were generally regarded as the simplest and presumably the most primitive group of the Homoptera. His views on the affinities of the groups comprising the Sternorrhyncha are based on the position of the beak in relation to the prosternum and according to him the Coccoidea are most closely related to the Aleyrodoidea.

Handlirsch (1908), who regards the Sternorrhyncha as a polyphyletic group and raises its four sub-families to the rank of sub-orders, also considers the Coccoidea to be highly specialized. In contrast to Osborn (1895) however, he regards the Psylloidea as being their nearest relatives and states that these two groups arose from a common ancestor, the Procercopidae. In his view the Aphidoidea is the most primitive of the Sternorrhyncha and together with the Aleyrodoidea, is far removed from the more specialized Psylloidea and Coccoidea. Handlirsch bases his conclusions on the relationships of the different groups on the structure of the antennae, wings and alimentary canal.

Kirkaldy (1910a, 1910b) is very much opposed to Handlirsch's views and he regards the Coccoidea as being closely related to the Aleyrodoidea. He further maintains that the Sternorrhyncha is a very compact group and should therefore be regarded as monophyletic.

Tillyard (1919) regards the Psylloidea as the oldest of the Sternorrhyncha and states that the Aphidoidea, Coccoidea and Aleyrodoidea are later and more specialized developments from the same stem as the Psylloidea. According to his phylogenetic tree the Coccoidea are more closely

related to the Aleyrodoidea and he therefore agrees with Kirkaldy (1910a) in this respect.

Singh-Pruthi (1925), on the basis of a study of the male genitalia, states that although the Coccoidea have a primitive type of penis, it is highly specialized in the structure of the rest of the genitalia. On the evidence provided by the structure of the penis alone, he assumes that the Coccoidea have arisen from the very base of the homopteran stem. Singh-Pruthi's views on the relationships of the Coccoidea cannot, however, carry much weight as they are based on the structure of a single organ in a single species of a group which he himself admits to be highly specialized in other respects.

Weber (1928, 1929, 1935a), in a series of papers on the comparative anatomy of *Psylla*, *Aphis* and Aleyrodids, often discusses the relationships of the various groups comprising the Sternorrhyncha, but he never makes any reference to the affinities of the Coccoidea (which he did not study). In his textbook (1933) he follows Handlirsch (1908) in regarding all the superfamilies of the Sternorrhyncha as sub-orders and equivalents of the whole of the Auchenorrhyncha.

Börner (1904, 1934) regards the coccids as being most closely related to the aphids and encloses these two groups in one superfamily. A similar arrangement is followed by Heymons (1915).

Spooner (1938), who studied the head capsule in Hemiptera (but not that of male coccids), places the Coccoidea near the Aleyrodoidea, thus following Kirkaldy (1910a) and Tillyard (1919). He, however, regards these two groups as far removed from the Psylloidea and Aphidoidea.

Evans (1942), in his paper on the phylogeny of the Hemiptera, makes no mention of the relationships of the Coccoidea.

The above remarks concerning the phylogeny of the Coccoidea and other Sternorrhyncha, indicate that there is still considerable controversy regarding the true relationships of the superfamilies of the Sternorrhyncha, mainly because none of the authors mentioned above had anything but the most fragmentary and superficial information about the morphology of male coccids on which to base their theories. One is indeed almost tempted to regard their opinions as little more than speculation, or at best, intuitive judgements unsupported by any serious body of fact. In the light of the anatomical information on male coccids, which is now available, together with the detailed studies of Weber on *Aphis*, *Psylla* and the Aleyrodoidea, a more profitable discussion of the relationships of the coccids seems possible. It must, however, be emphasized that the conclusions and discussion which follow, are based almost entirely on the information provided by the 7 species which I have studied and the 3 investigated by Weber. To what extent the characters which they show are really representative of the groups to which they belong, cannot be fully appreciated as yet and further work will undoubtedly be necessary to test the phylogenetic suggestions which are made tentatively here. At the same time, I believe that the range of characters available to me and the detail in which they have been studied is far greater than that used by the older authors and that any dissent from the suggestions which are made here should at least be based on an equally intensive study.

Apart from Singh-Pruthi (1925), all authors are agreed that the Coccoidea are a very specialized group and this is also borne out by a study of the morphology of the male. The loss of functional mouthparts, the reduction of the hind wings to halteres, the development of postnotal apophyses and the relative simplicity of the external genitalia are all important specializations which are not found in any of the other Homoptera. To these anatomical specializations of male coccids may also be added their distinctive type of metamorphosis, which was called parametaboly by Börner (1910) but has recently been described as true holometaboly by Bodenheimer (1951). As was pointed out previously in the general discussions on the structure of the head, thorax and abdomen (see pp. 18, 43, 53), *Margarodes* is undoubtedly the most primitive of the male coccids studied and a detailed study of its morphology also indicates that it is probably more closely related to the Aphidoidea than to any of the other Sternorrhynchan superfamilies, thus lending support to the theories of Börner (1904, 1934) and Heymons (1915).

The following important characters are common to both *Margarodes* and *Aphis* but are not found in *Psylla* and aleyrodids:

(1) The presence of small persistent larval eyes in the adult. In *Aphis* three of these larval eyes are situated close together behind each compound eye, but in *Margarodes* there is apparently only one behind each compound eye. Pflugfelder (1937), however, states that in *Eulecanium* the unicorneal eyes consist of three ommatidia and similar conditions probably obtain in *Margarodes*.

(2) The attachment of antennal muscles to the cranial wall.

(3) The development of a posttergite in the prothorax.

(4) The prolongation of the postalare of the mesopostnotum and its articulation with the pleural region. In aleyrodids and *Psylla* the postalare is short and indistinguishably fused to the epimeron (Weber, 1935a, 1929).

(5) The elimination of the first abdominal sternite.

(6) Apart from a slight reduction in the extent of the epimeron in *Margarodes*, the mesopleuron of *Aphis* is almost identical with that of *Margarodes*. In both of them a subepisternal ridge and lateropleurite is present and the mesopleural ridge is also well developed. In *Psylla* the mesopleural ridge is very short and in aleyrodids it is apparently not developed.

(7) In *Margarodes* the pronotum is not connected to the propleuron and although there is a weak connection between these two parts in *Aphis*, it is still very different from the broad fusion which is found in *Psylla* and aleyrodids.

(8) In the metasternum the two sternal apophyses are widely separated from one another.

(9) The metathorax and hind wings of *Aphis* are much reduced in size, although not to the same extent as in *Margarodes*.

(10) Pulvilli and arolia are absent from the pretarsus.

In spite of its resemblances to *Aphis*, *Margarodes* also has some characters in common with aleyrodids and there is therefore some justification for the views of Osborn (1895), Kirkaldy (1910a), Tillyard (1919) and Spooner (1938), who regard the Aleyrodoidea as the nearest relatives of the Coccoidea.

The following characters are shared by aleyrodids and *Margarodes*, but are absent in *Aphis* and *Psylla*:

- (1) The presence of a postoccipital ridge.
- (2) The presence of muscles extending from the postoccipital ridge directly to the mesoprephragma, thus eliminating separate neck muscles.
- (3) The presence of a separate cervical sclerite. The cervical sclerite of *Margarodes* is however intimately associated with the pleural ridge and is not as independent as that of aleyrodids.
- (4) Absence of a trochantin.
- (5) The presence in aleyrodids of a small projection which may be homologous with the postnotal apophysis of *Margarodes*.
- (6) The presence of an unpaired basal process of the penis. It is however likely that similar conditions obtain in *Aphis*, but the information is not available.

(7) It may also be said that the absence of a frontal ocellus in aleyrodids is a step in the direction of the margarodid condition, where all the dorsal ocelli are absent. *Aphis* and *Psylla* have retained three dorsal ocelli.

With *Psylla*, *Margarodes* has nothing in common apart from the general homopteran characters and there is therefore no justification for regarding the Coccoidea as closely related to the Psylloidea. The following features are shared by *Margarodes*, *Aphis* and aleyrodids, but not by *Psylla*:

(1) In *Margarodes*, *Aphis* and aleyrodids the mouth opening is situated near the posterior margin of the head and the head is therefore not as opisthognathous as in *Psylla*.

(2) Distinct larval eyes persist in the adults of *Margarodes* and *Aphis* and Pflugfelder (1937) states that traces of them are also retained in adult aleyrodids. In *Psylla* they are completely absent.

(3) The propleural ridge is well developed in *Psylla* but very short in the other three superfamilies.

(4) In *Psylla* the prealare is fused to the episternum, whereas in *Margarodes*, *Aphis* and aleyrodids it articulates with the episternum.

(5) The mesopostphragma of *Margarodes*, *Aphis* and aleyrodids is undivided, but in *Psylla* it is divided into two long plates.

(6) A mesosternal coxal articulation is present in *Psylla*, but is absent in the other groups.

(7) In *Margarodes*, *Aphis* and aleyrodids the penis is a relatively simple tubular structure, but in *Psylla* it is more complex and its distal part is movably connected to the basal part (Weber, 1930).

The conclusions drawn from the above comparisons of the anatomical features of the Sternorrhynchan superfamilies, can be summarized as follows:

(a) The Coccoidea are a highly specialized group but are more closely related to the Aphidoidea than to any of the other Sternorrhynchan groups.

(b) The Coccoidea also have much in common with the Aleyrodoidea, but this is only to be expected since Weber (1928, 1935a) regards the Aleyrodoidea as not far removed from the Aphidoidea.

(c) Contrary to the theories of Handlirsch (1908), it is quite clear that the Psylloidea are far removed from the Coccoidea. This is also in accordance with the views of Weber (1935) who states that the Psylloidea are not closely related to either the Aleyrodoidea or Aphidoidea.

B. AFFINITIES OF SUBDIVISIONS OF COCCOIDEA.

The relationships of the various subdivisions of the Coccoidea have in the past received very little attention and in the majority of the considerable number of papers on the classification of the Coccoidea, e.g. those by Green (1896—1909), Lindinger (1912), Leonardi (1920), MacGillivray (1921), Ferris (1937) and Silvestri (1939), the natural relationships of the groups are almost completely ignored. As all these classifications are based almost solely on the anatomy of the highly specialized neotenic females, it is not perhaps surprising that the authors found it difficult to determine the true affinities of the groups.

In 1937 Balachowsky published a paper in which he discusses the anatomy of male coccids and also states that they can be divided into three distinct types, namely the diaspidoids, lecanoids and margaroids. Jancke (1955) follows the same arrangement. In a later paper (1942) Balachowsky elaborates this theory so as to include the females and also indicates the relationships between the groups. He separates the males of these groups according to the following key:

- | | | | |
|--|-----|-----|----------------------|
| (1) Abdominal spiracles present | ... | ... | phylum Margaroidae. |
| Abdominal spiracles absent | ... | ... | 2. |
| (2) Head separated from thorax by neck | ... | ... | phylum Lecanoidae. |
| Head fused with thorax | ... | ... | phylum Diaspidoidae. |

Although Balachowsky therefore bases his classification, as far as the males are concerned, only on the degree of fusion between head and thorax and the presence or absence of abdominal spiracles, I find that his views are also corroborated by a much more thorough morphological study, as will be shown presently. Of the male coccids which I have studied, *Margarodes*, *Pseudaspidopectus* and *Steingelia* belong to the margaroid type, *Eulecanium* and *Pseudococcus* to the lecanoid type and *Aulacaspis* and *Diaspidiotus* to the diaspidoid type.

(a) *Margaroid type.*

According to Balachowsky (1942) the margaroid type or phylum Margaroidae, as he calls it, is primitive and he regards the Ortheziidae as its most primitive representative, a view also held by Handlirsch (1925). Prior to the publication of his paper, the primitiveness of the margaroid group was generally agreed upon, mainly because of the presence of compound eyes and addominal spiracles in the adult male. Many other primitive features are however also present in this group. As was pointed out previously, *Steingelia* is rather aberrant in some respects, but the following characters of *Margarodes* and *Pseudaspidopectus* are distinctly primitive when compared with the other coccids studied:

- (1) The head and thorax are about as well separated as in aphids and aleyrodids.
- (2) The presence of compound eyes.
- (3) Sclerite degeneration is less advanced than in other species.
- (4) The ventromedial part of the epicranium is large and heavily sclerotized.

- (5) The presence of a small pronotum and the absence of pronotal ridges.
- (6) The presence of large posttergites with internal ridges.
- (7) The boundary between the cervical sclerite and the pleural ridge can still be distinguished.
- (8) The prescutal ridges are situated far laterally so that the prealares arise from the prescutum.
- (9) The distal part of the prealare is not modified into a triangular plate.
- (10) The scutellum extends laterally to the margin of the notum and is bounded anteriorly by a typical V-shaped scutoscuteellar suture.
- (11) The presence of metathoracic sternal apophyses.
- (12) The presence of broad halteres.
- (13) The presence of abdominal spiracles.
- (14) The shortness of the connection between the penis and the floor of the penial sheath is probably also a primitive feature, but it is impossible to be definite about this, as the information about conditions in *Aphis* is lacking.

Pflugfelder (1939) states that the monophlebids are the most primitive coccids, but this is probably not true since *Pseudaspidoproctus* is more specialized than *Margarodes* in the following respects:

(1) Sclerite degeneration is much more marked in *Pseudaspidoproctus* than in *Margarodes*. In *Pseudaspidoproctus* the head is only well sclerotized ventrally, a propleural sclerite and lateropleurite is absent, the mesonotum contains large membranous areas and the abdominal tergites and sternites have been reduced to narrow strips.

(2) Preocular, postocular and preoral ridges are present in *Pseudaspido- proctus* but absent in *Margarodes*.

(3) A short cranial apophysis is present in *Pseudaspido- proctus* but completely absent in *Margarodes*.

(4) The presence of caudal appendages in *Pseudaspido- proctus*.

(5) The external genitalia of *Pseudaspido- proctus* are very different from those of *Margarodes* and probably more specialized.

Of these characters the first three are very important since they apparently mark the beginning of specializations which are carried to extremes in the more highly specialized Coccoidea. In only one respect, namely the presence of two small propleural apophyses, does *Pseudaspido- proctus* appear to be more primitive than *Margarodes*.

The relationships of *Steingelia* are problematic. Although it is usually included in the family Margarodidae, it is very specialized and differs from *Pseudaspido- proctus* and *Margarodes* in the following respects:

(1) The replacement of the compound eyes by a row of simple eyes on each side.

(2) The extreme opisthognathy of the head and the caudal migration of the tentorial arms.

(3) The presence of a long arm-like cranial apophysis very similar to that found in the more specialized coccids.

- (4) Very pronounced sclerite degeneration.
- (5) The presence of a deep cervical groove and distinct neck similar to that found in *Pseudococcus* and *Eulecanium*.
- (6) The presence of a pronotal ridge comparable to that of *Pseudococcus* and *Eulecanium*.
- (7) Complete fusion of the pleural ridge and cervical sclerite to form a structure comparable to that of the more specialized coccids.
- (8) Modification of the distal part of the prealare into a triangular plate identical to that found in *Eulecanium*, *Pseudococcus*, *Aulacaspis* and *Diaspidiotus*.
- (9) The presence of a tubular scutellum like that found in *Eulecanium taxi*, *Aulacaspis* and *Diaspidiotus*.
- (10) As in *Eulecanium* and *Pseudococcus* a distinct postoccipital ridge is absent.
- (11) The presence of small mesosternal sclerites which may be vestiges of a sternal articulation of the coxae.

This last character, as well as the extreme opisthognathy of the head, are not found in any of the other coccid species studied and their agreement with conditions in *Psylla*, is probably due to convergence. From the above list of characters it is clear that *Steingelia* has a considerable number of important specialized characters in common with *Eulecanium*, *Pseudococcus* and the Diaspididae and Green (1917) is therefore perfectly justified in having doubts about the inclusion of this genus in the family Margarodidae. On the other hand it also shares the following primitive characters with *Margarodes*.

- (1) Presence of abdominal spiracles.
- (2) Absence of postocular ridges (it is possible that these ridges were lost secondarily).
- (3) The anterior tentorial arms are not associated with the cranial apophysis.
- (4) The prealare arises from the prescutum.
- (5) Presence of a large lateropleurite.
- (6) Presence of metasternal apophyses.
- (7) The penis of *Steingelia* is more like that of *Margarodes* than that of any other group.

Steingelia is therefore on the one hand related to *Margarodes* but on the other hand also shows affinities with the more specialized Coccoidea, especially *Eulecanium* and *Pseudococcus*. Green's (1920) contention that the male of *Steingelia* constitutes a connecting link between the Margarodidae and Pseudococcidae, is therefore quite plausible and it is doubtful if this genus should remain in the family Margarodidae.

(b) *Lecanoid type*.

According to Balachowsky (1942) this group, which he calls the phylum Lecanoidae, is less homogeneous and more specialized than the previous group and both he and MacGillivray (1921) state that it is connected to the

margaroids through the family Phenacoleachidae. As was shown previously, however, *Steingelia* may perhaps also be regarded as a connecting link between these two groups.

The two genera, which were studied, *Eulecanium* and *Pseudococcus*, are distinctly separate from the margaroid type and exhibit the following specialized characters when compared with that group (excluding *Steingelia* whose relationships with the lecanoids have already been discussed):

- (1) The presence of simple dorsal and ventral eyes.
- (2) The presence of a distinct, constricted neck region.
- (3) Absence of a distinct postoccipital ridge and the attachment of the prothoracic muscles to the posterior edge of the dorsomedial part of the epicranium.
- (4) Presence of lateral branches of the midcranial ridge.
- (5) The prolongation of the cranial apophysis and the association of the latter with the anterior tentorial arms.
- (6) Presence of pronotal ridges.
- (7) Complete fusion of the cervical sclerites and pleural ridge to form a ridge-like structure.
- (8) The prescutal ridges have shifted medially and the prelares therefore arise from the scutum.
- (9) Absence of metasternal sclerotizations or apophyses.
- (10) Absence of abdominal spiracles and most of the tergal and sternal abdominal plates.

When *Eulecanium* and *Pseudococcus* are compared with one another, the latter is seen to be probably the more primitive mainly because of the very specialized condition of the external genitalia in *Eulecanium*. The absence of a posttergite and a basalar are probably also specializations in the latter. Morrison is therefore probably correct when he states that the Pseudococcidae are the closest relatives of the Margarodidae. On the other hand, the fusion of the anterior tentorial arms with each other and the preocular suture with the postocular suture, are minor specializations which are present in *Pseudococcus* but not in *Eulecanium*.

(c) *Diaspidoid type*.

According to Balachowsky (1942) this type is not closely related to the lecanoids. This statement is however not confirmed by a detailed study of the morphology of the male since most of the specializations listed in *Eulecanium* and *Pseudococcus* are also present in *Aulacaspis* and *Diaspidiotus*. It can therefore be said that the diaspidoids are probably more closely related to the lecanoids than the latter are to the margaroids.

Aulacaspis and *Diaspidiotus* differ from the lecanoids in the following points:

- (1) The head is intimately associated with the prothorax.
- (2) A postoccipital ridge is present; this is probably a primitive feature.

(3) The heavily sclerotized penial sheath and penis of diaspidids have very little resemblance to the external genitalia of *Eulecanium* and *Pseudococcus* and are definitely more specialized.

(4) A tentorium is completely absent.

(5) Complete absence of a propleural apophysis.

(6) The almost complete desclerotization of the head, apart from the ridges.

(7) Absence of epimera.

The last five characters are all specializations and they indicate that the diaspidoids are probably more specialized than the lecanoids, although the presence of a postoccipital ridge in the former is a primitive feature. These two groups probably developed from a common ancestor and the diaspidoids probably did not arise from the lecanoids as Balachowsky's (1942) diagram indicates.

Diaspidiotus and *Aulacaspis* are very closely related, but the complete absence of lateral ocelli and pronotal ridges in the latter, seems to indicate that it is more specialized than *Diaspidiotus*.

VII. S U M M A R Y.

(1) The male Coccoidea are specialized and are characterized by the loss of functional mouth parts and dorsal ocelli, the reduction of the hind wings to halteres and the desclerotization of the greater part of the body wall.

(2) Seven species of coccids, belonging to different subfamilies were studied. Of these the margarodids are probably the most primitive since they possess large compound eyes (except *Steingelia*), abdominal spiracles and metasternal apophyses. Sclerite degeneration is also less advanced than in the other species and the thorax is very similar to that of the other Sternorrhynchan Homoptera.

(3) Separate neck muscles are absent dorsally and the prothoracic muscles extend between the mesoprephragma and the postoccipital ridge.

(4) Antennal muscles are completely detached from the anterior tentorial arms and have become secondarily attached to the ventral cranial wall (*Margarodes*) or the cranial apophysis, which is an invagination of the ventral cranial wall.

(5) The epicranium consists of a medial part and two lateral ocular sclerites.

(6) Larval eyes persist in the adult as so-called lateral ocelli and in all the species studied, except *Margarodes* and *Pseudaspidopectus*, the compound eyes are absent and replaced by simple eyes.

(7) In all the species studied, except *Margarodes*, the head capsule is reinforced by secondary preocular, postocular and preoral ridges.

(8) A tentorium is present in all species, except *Aulacaspis* and *Diaspidiotus*. In *Eulecanium* and *Pseudococcus* the anterior arms of the tentorium are associated with the cranial apophysis.

(9) In *Margarodes* and *Pseudaspidopectus* a small pronotum is present, but in the other species it has been replaced by ridge-like structures, the pronotal ridges.

(10) The pleural region of the prothorax is very poorly developed. Episterna and epimera can never be distinguished and the cervical sclerite is either intimately associated with the pleural ridge or completely fused with it.

(11) The mesothorax is not very specialized and is fairly similar to that of *Aphis*.

(12) In *Margarodes* and *Pseudaspidopectus* the scutellum is primitive, but in *Steingelia*, *Eulecanium* and the diaspidids it is transformed into a tubular structure with a ventral scutellar foramen.

(13) The mesopostnotum is overlapped by the metathorax and possesses internal postnotal apophyses and elongate postalares, the latter articulating with the mesopleural ridges.

(14) The scutellum is movably connected to the mesopostnotum.

(15) The articulation of the wings is very similar to that of other Hemiptera.

(16) The sternopleural region of the mesothorax is strengthened by sub-episternal, marginal and precoxal ridges.

(17) The mesosternal plate represents a basisternum and posteriorly bears a well developed furca.

(18) The metathorax is very much reduced and two small suspensorial sclerites are found at the base of the halteres.

(19) In *Margarodes* well developed abdominal tergites and sternites are present but in the other species the pregenital segments are largely desclerotized

(20) The external genitalia consist only of a penis and penial sheath, periphallid structures being absent.

(21) The penial sheath probably represents the enlarged lateral parts of the 9th abdominal sternum.

(22) In *Eulecanium* and the diaspidids the penis and penial sheath are prolonged into a stylus.

(23) A long median basal plates prolongation is present in *Pseudococcus* and the diaspidids.

(24) In general it can be said that the Coccoidea are more closely related to the Aphidoidea than to any of the other Sternorrhyncha. They have some characters in common with the Aleyrodoidea, but are far removed from the Psylloidea.

(25) Balachowsky's (1937, 1942) subdivision of the Coccoidea into three types, the margaroids, lecanoids and diaspidoids, is supported by a detailed morphological study of the male. The margaroids are the most primitive and the diaspidoids the most specialized group.

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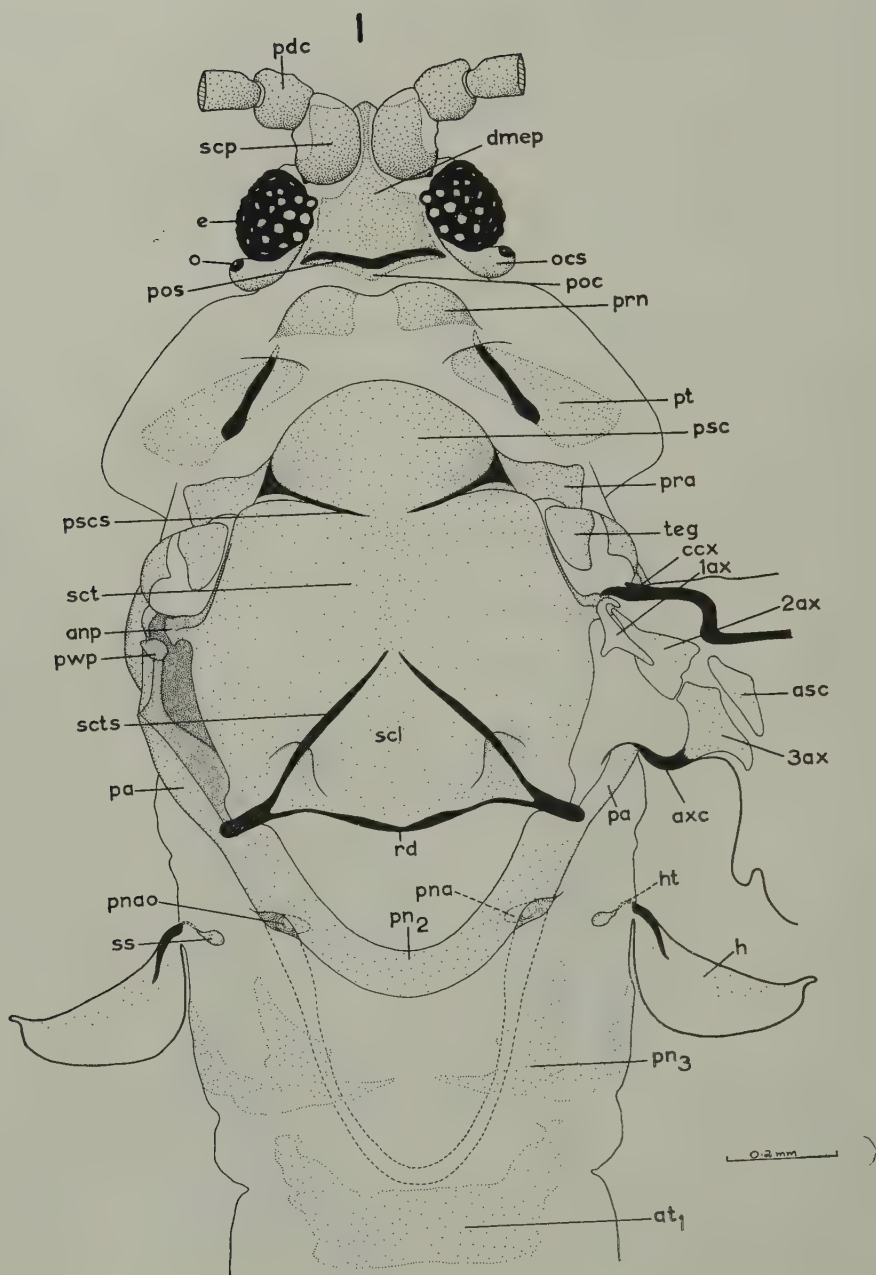
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 Fig. 27. — *Diaspidiotus bavaricus* Lind., lateral view of head and thorax.
 Fig. 28. — *Margarodes vitium* Giard, lateral view of abdomen.
 Fig. 29. — *Pseudaspidoproctus* (?) *fulleri* (Ckll.), lateral view of genitalia.
 Fig. 30. — *Pseudaspidoproctus* (?) *fulleri* (Ckll.), ventral view of genitalia.
 Fig. 31. — *Margarodes vitium* Giard, ventral view of genitalia.
 Fig. 32. — *Steingelia gorodetskia* Nasonow, lateral view of genitalia.
 Fig. 33. — *Pseudococcus citri* (Risso), lateral view of genitalia.
 Fig. 34. — *Eulecanium taxi* Habib, ventral view of genitalia.
 Fig. 35. — *Margarodes vitium* Giard, middle leg.
 Fig. 36. — *Margarodes vitium* Giard, front leg.
 Fig. 37. — *Pseudaspidoproctus* (?) *fulleri* (Ckll.), hind tarsus.
 Fig. 38. — *Steingelia gorodetskia* Nasonow, hind tarsus.
 Fig. 39. — *Eulecanium taxi* Habib, hind tarsus.
 Fig. 40. — *Pseudococcus citri* (Risso), hind tarsus.
 Fig. 41. — *Aulacaspis pentagona* (Targ.), hind tarsus.
 Fig. 42. — *Diaspidiotus bavaricus* Lind., hind tarsus.

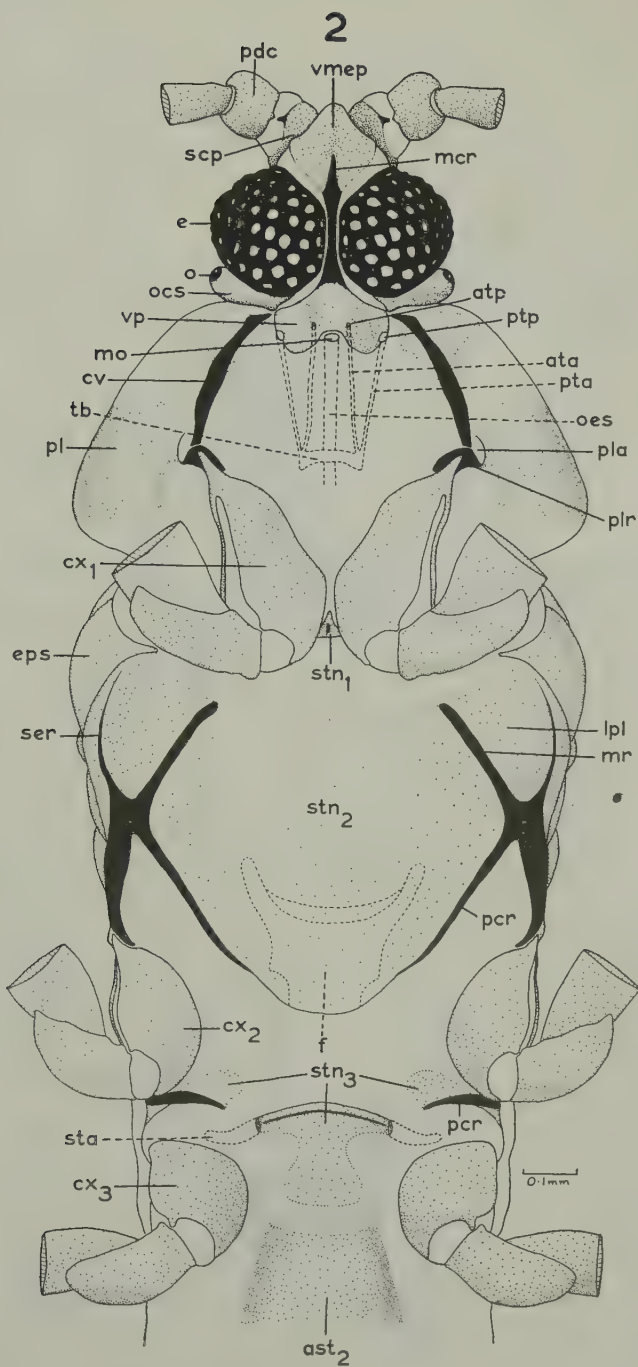
XI. LIST OF ABBREVIATIONS

a	= apodeme
AI-VIII	= abdominal segments I-VIII
an	= anus
anp	= anterior notal wing process
ant	= antenna
ant mscls.	= antennal muscles
ant. n.	= antennal nerve
asc	= additional sclerite
ast	= abdominal sternite
at	= abdominal tergite
ata	= anterior tentorial arm
atp	= anterior tentorial pit
ax	= axillary sclerite
axc	= axillary cord
ba	= basalare
br	= brain
bra	= basal rod of penis
ca	= cranial apophysis
cao	= external opening of cranial apophysis
cap	= caudal appendage
ccx	= costal complex of veins
ce	= caudal extension
cl	= tarsal claw
cv	= cervical sclerite
cx	= coxa
dej	= ductus ejaculatorius
dmep	= dorsomedial part of epicranium
dse	= dorsal simple eye
e	= compound eye
epic	= epicranium
epm	= epimeron
eps	= episternum
f	= furca
fm	= femur
fp	= furcal pit
g	= gena
gl	= gland
h	= haltere
ht	= tendon attached to haltere
iga	= internal genital aperture

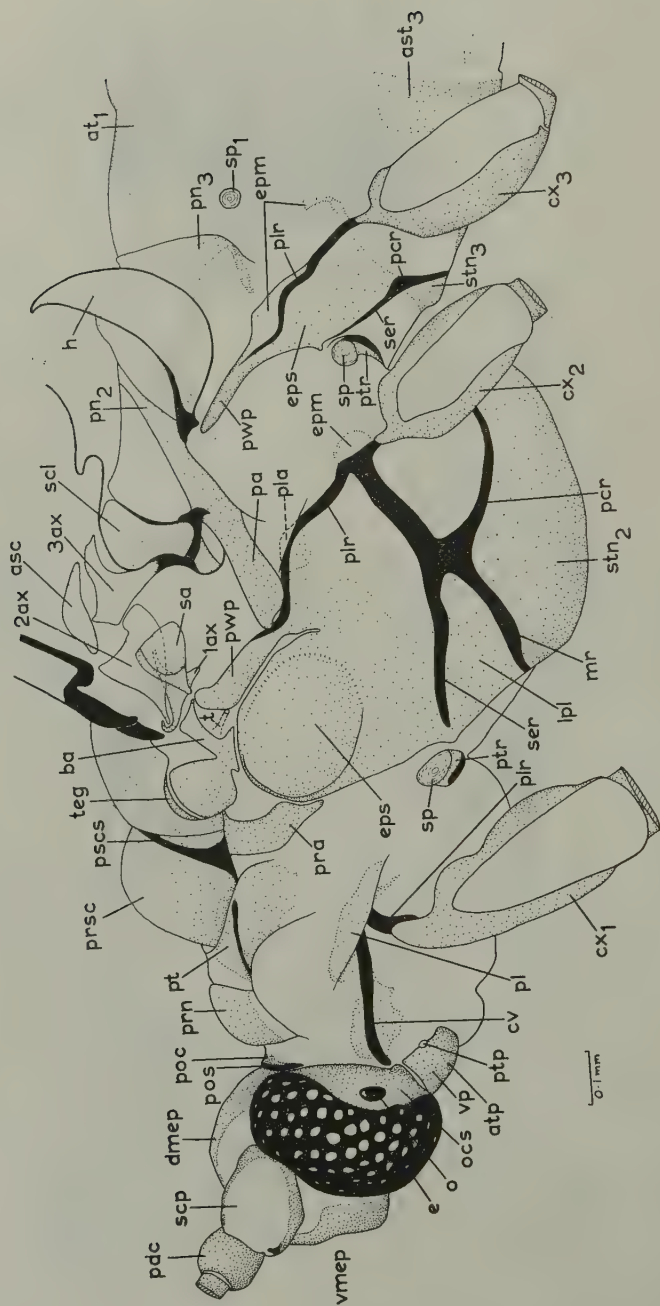
lmc _r	= lateral branch of midcranial ridge
lpl	= lateropleurite
mc	= median crest
mcr	= midcranial ridge
mo	= mouth opening
mr	= marginal ridge
mt	= mouth tubercle
mtn	= metanotum
o	= lateral ocellus
ocs	= ocular sclerite
oes	= oesophagus
opl	= optic lobe
p	= posterior projection of ocular sclerite
pa	= postalare
pcr	= precoxal ridge
pdc	= pedicel
pen	= penis
phr ₁	= mesoprephragma
phr ₂	= mesopostphragma
pl	= pleuron
pla	= pleural apophysis
plev	= propleuron + cervical sclerite
plr	= pleural ridge
pn ₂	= mesopostnotum
pn ₃	= metapostnotum
pna	= postnotal apophysis
pnao	= external opening of postnotal apophysis
pnp	= posterior notal wing process
poc	= postocciput
pocr	= postocular ridge
por	= postoccipital ridge
pos	= postoccipital suture
pr	= projection of penial sheath
pra	= prealare
prn	= pronotum
prnr	= pronotal ridge
pro	= process of penial sheath
procr	= preocular ridge
pror	= preoral ridge
prsc	= prescutum
ps	= penial sheath
pscr	= prescutal ridge

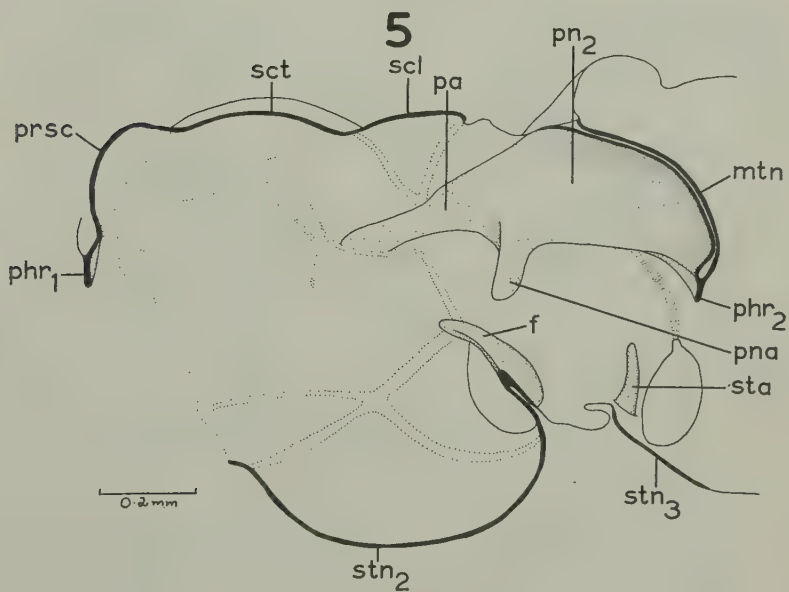
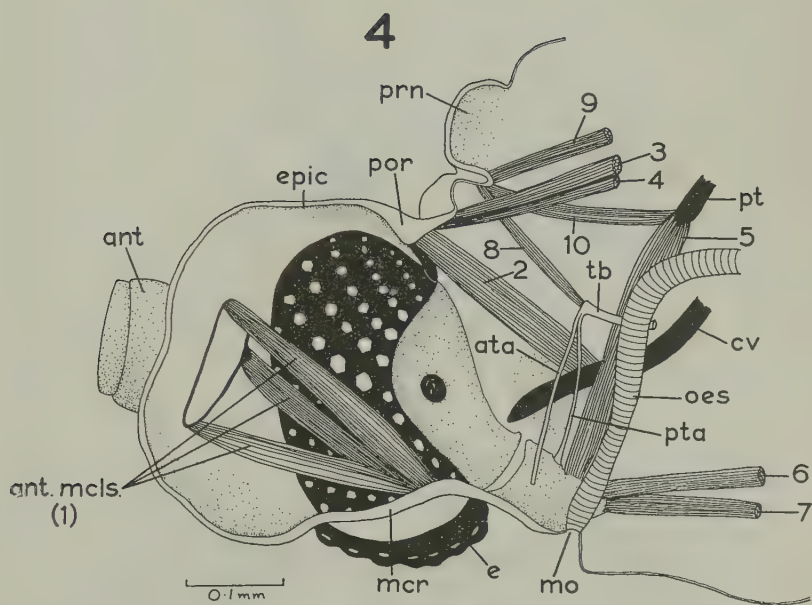
pacs	= prescutal suture
pt	= posttergite
pta	= posterior tentorial arm
ptp	= posterior tentorial pit
ptr	= peritreme
pwp	= pleural wing process
rd	= posterior marginal fold of notum
rec	= rectum
s	= sclerite of unknown homology
sa	= subalare
scl	= scutellum
scf	= scutellar foramen
scp	= scape
set	= scutum
sets	= scutoscuteellar suture
sd	= duct of salivary gland
se	= simple eye
ser	= subepisternal ridge
sp	= spiracle
ss	= suspensorial sclerites of halteres
st	= stylus
sta	= sternal apophysis
stn	= sternum
t	= tendon-like apodeme
tar	= tarsal segment
tb	= tentorial bridge
teg	= tegula
tib	= tibia
tp	= triangular plate of prealare
tr	= trochanter
vc	= ventral cavity
vmep	= ventromedial part of epicranium
vp	= ventral plate
vs	= ventral sclerite
vse	= ventral simple eye



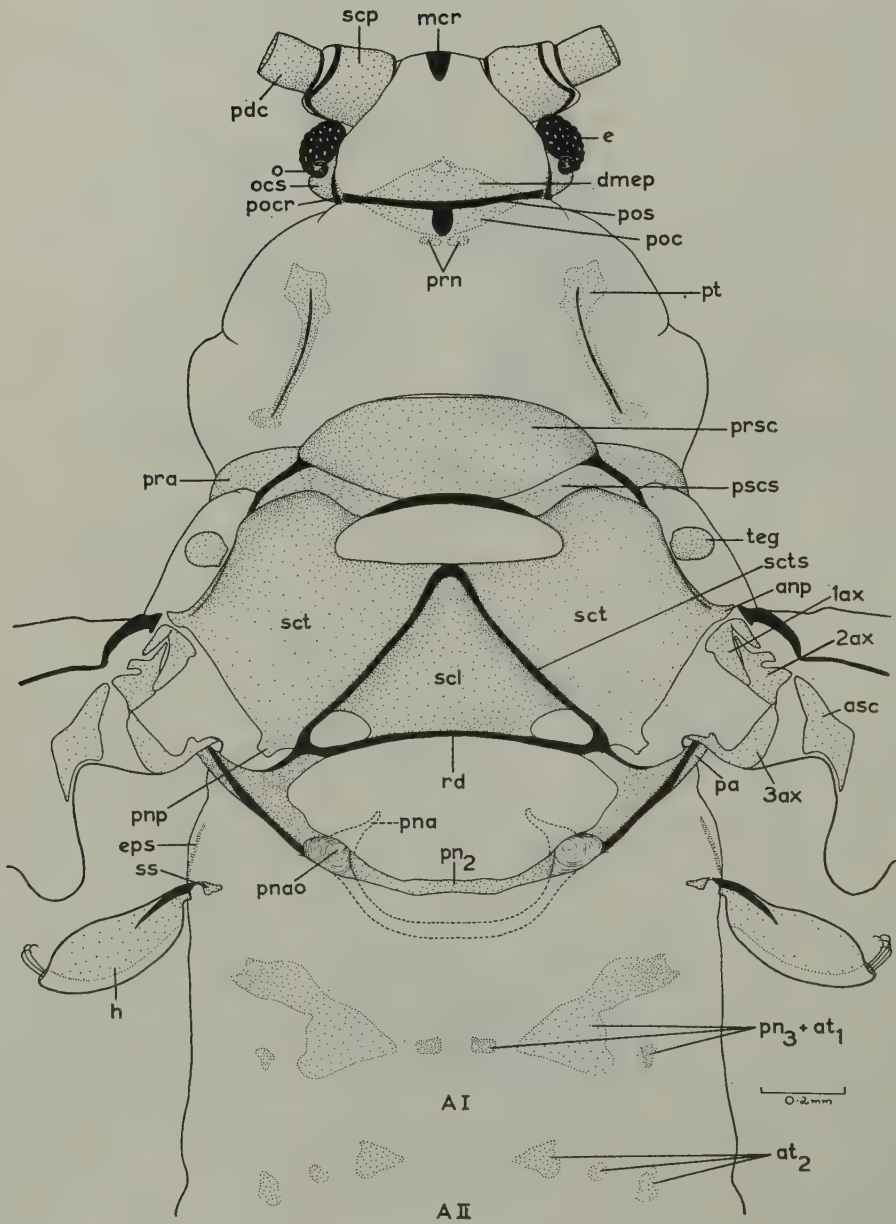


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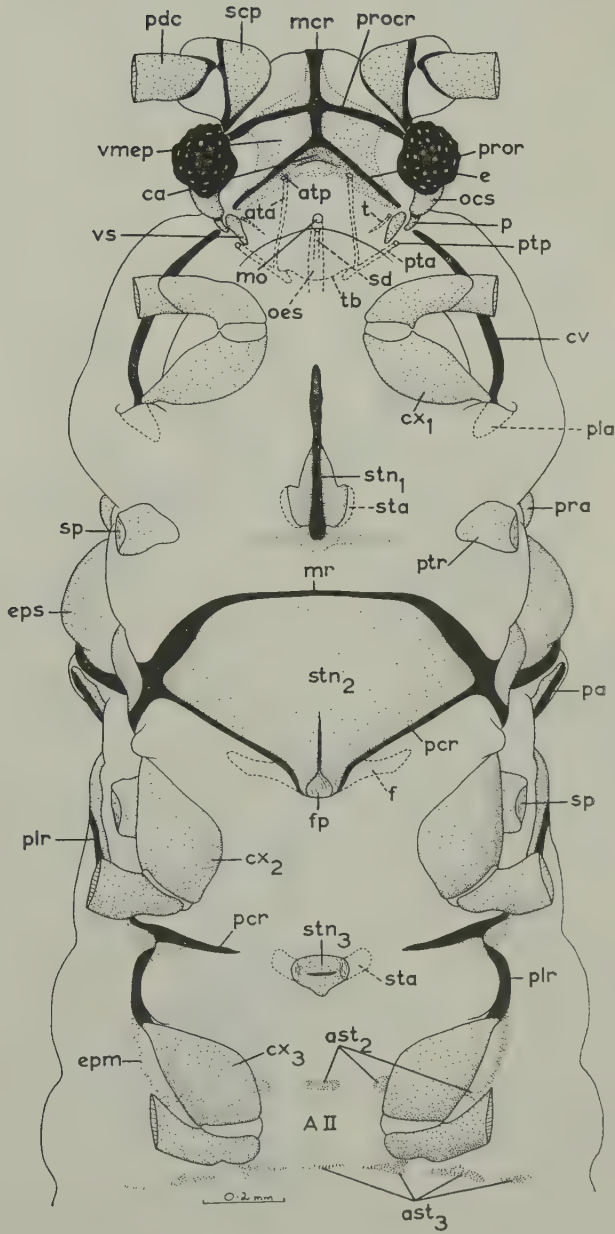


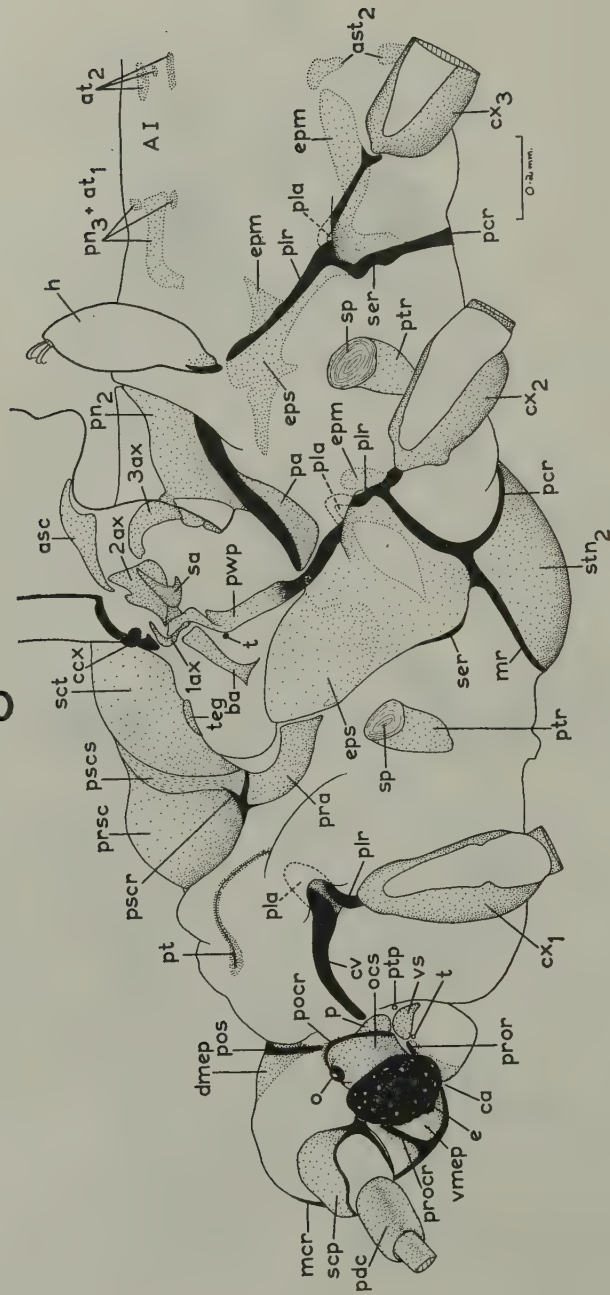


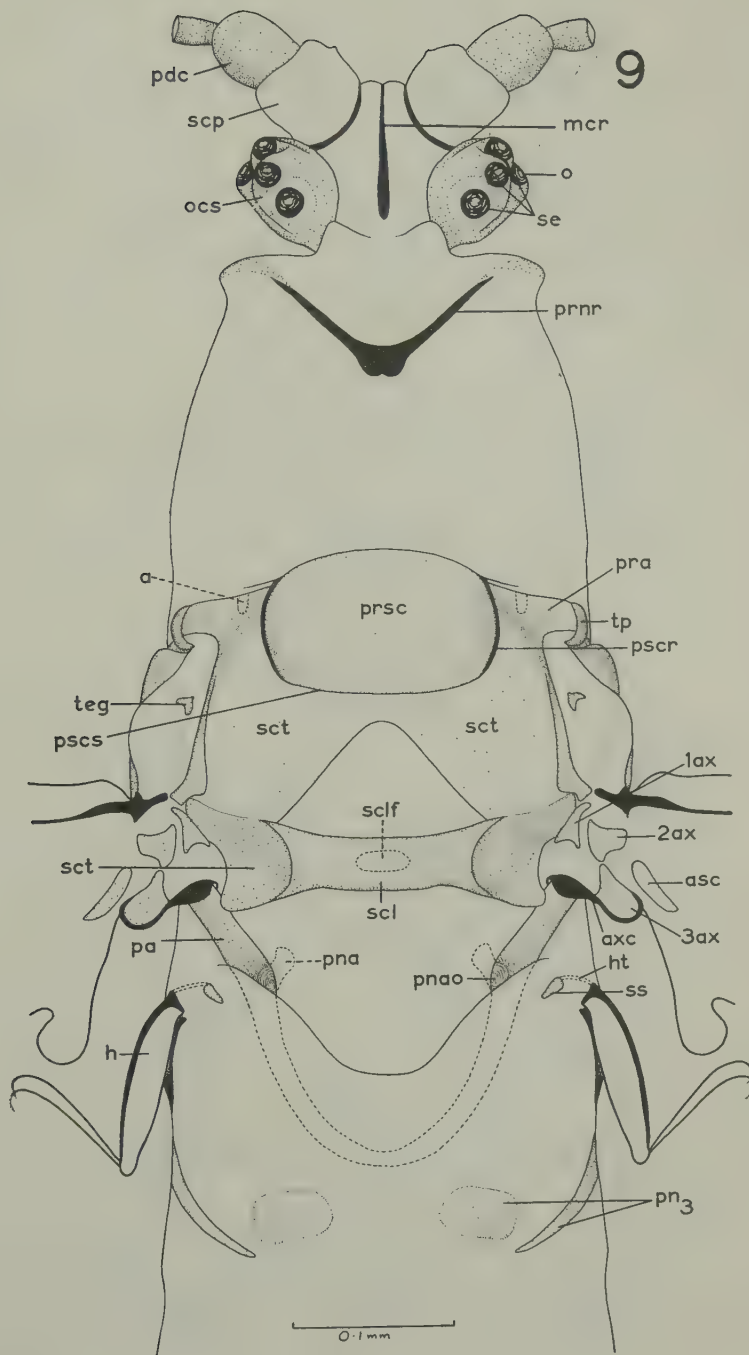
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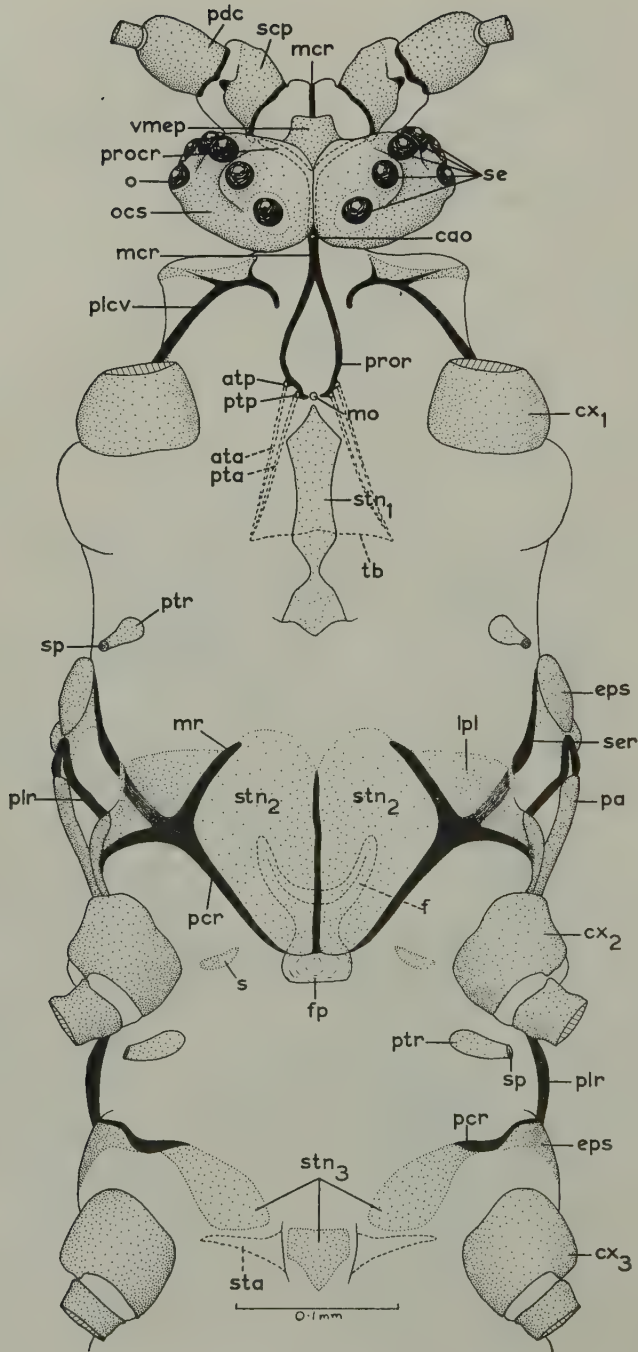
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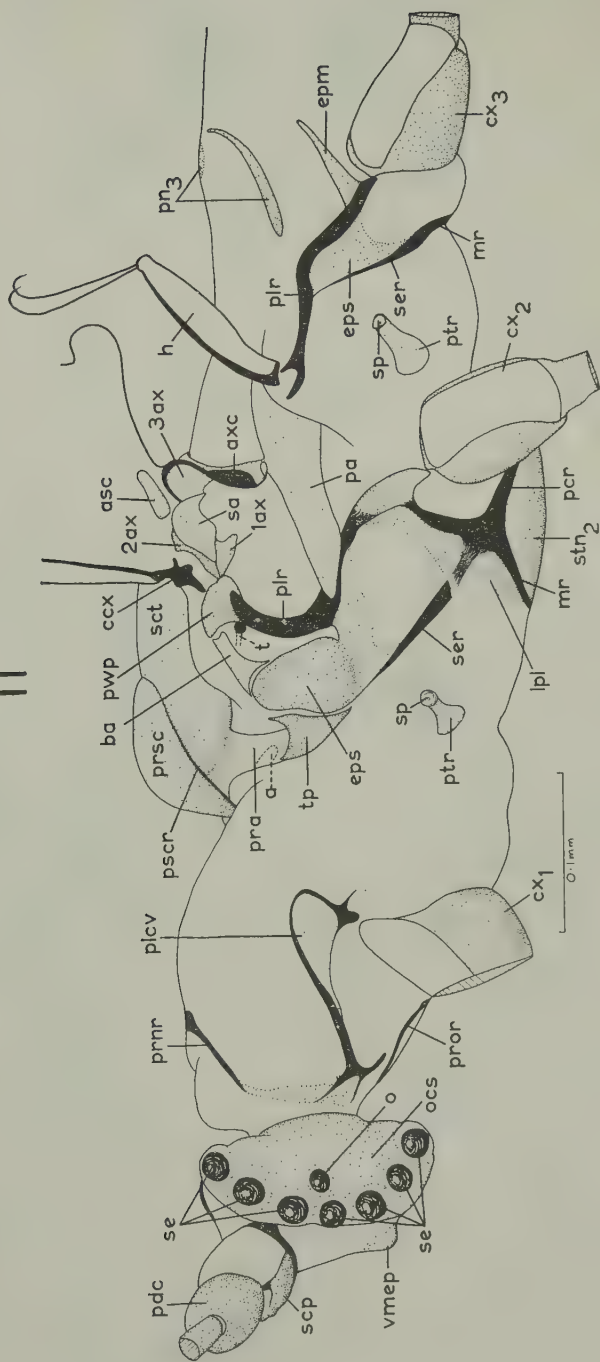


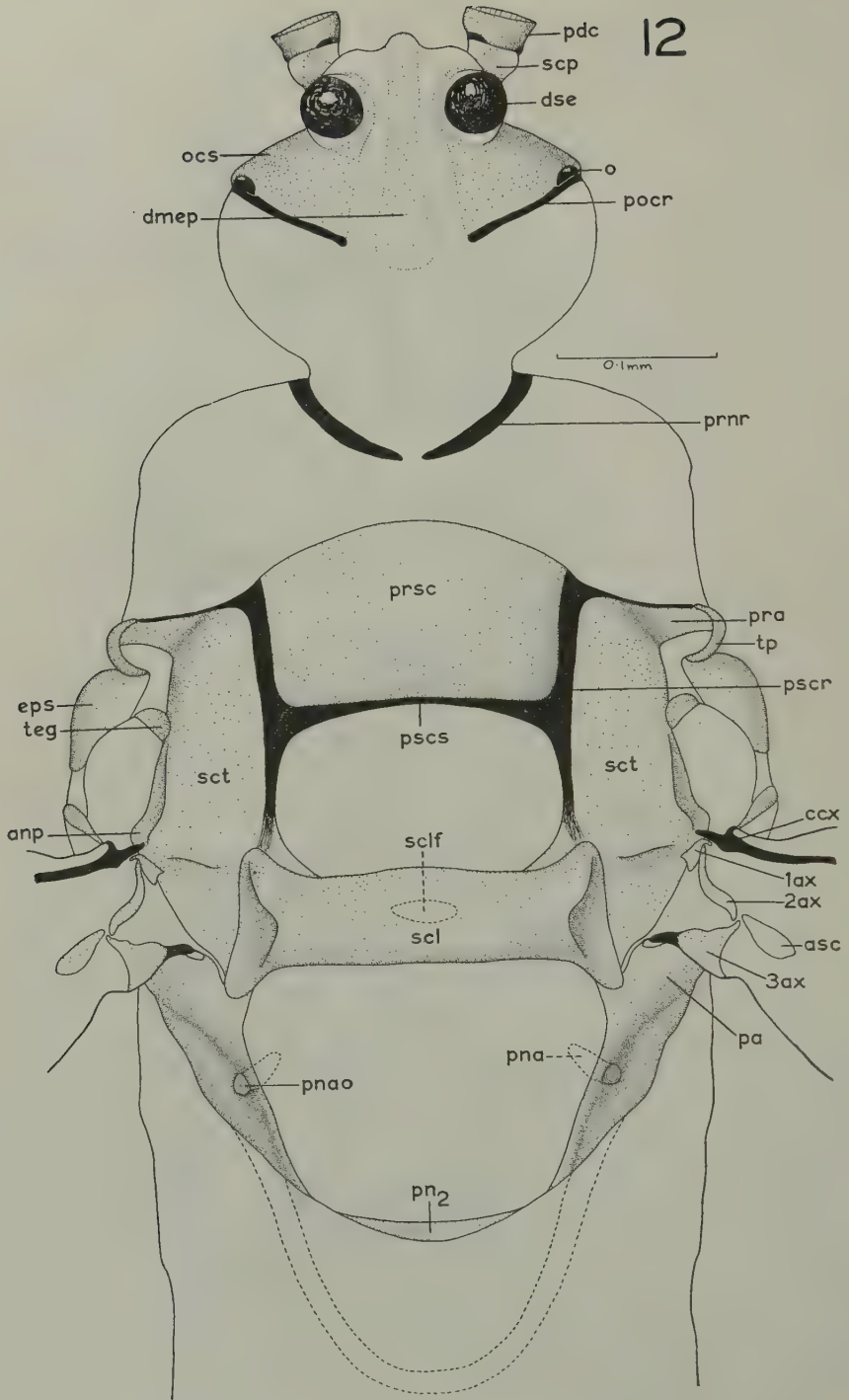


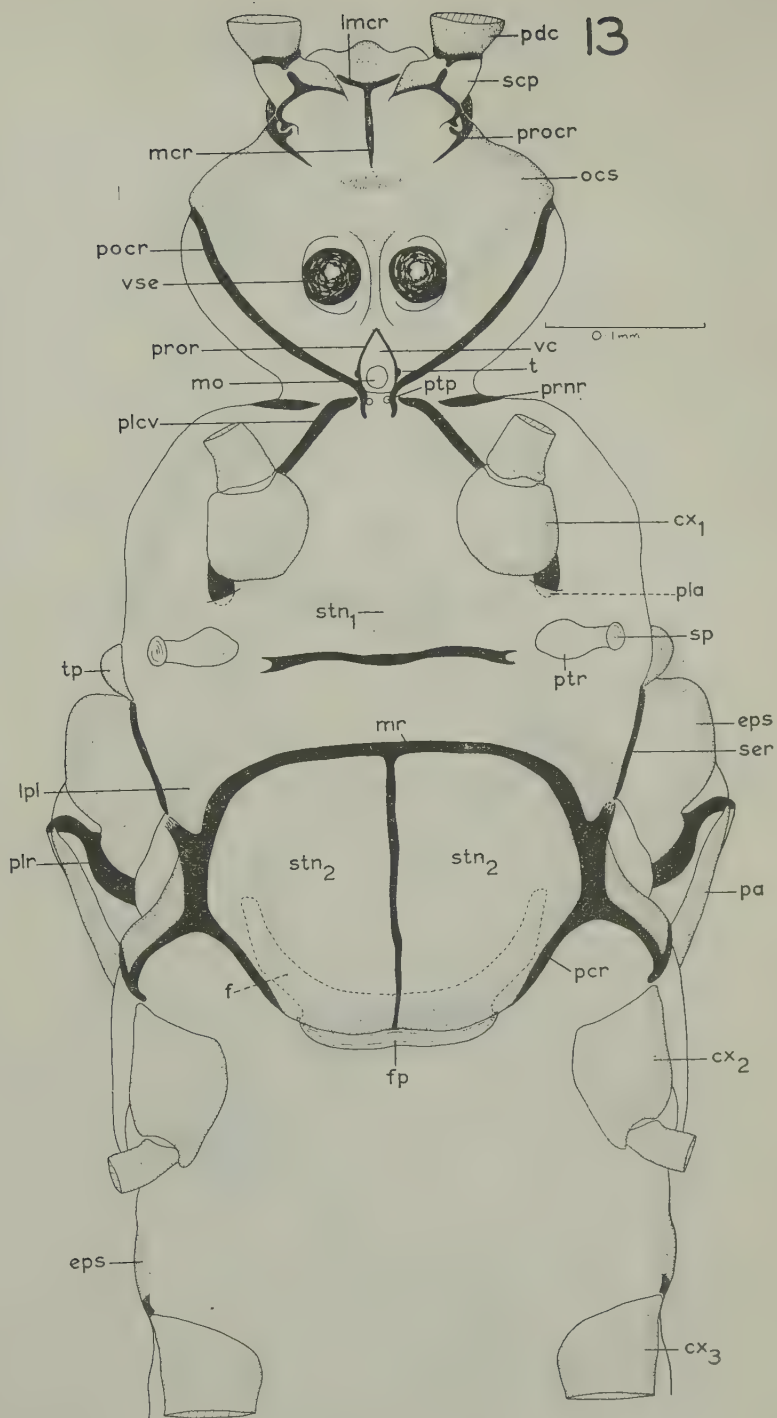
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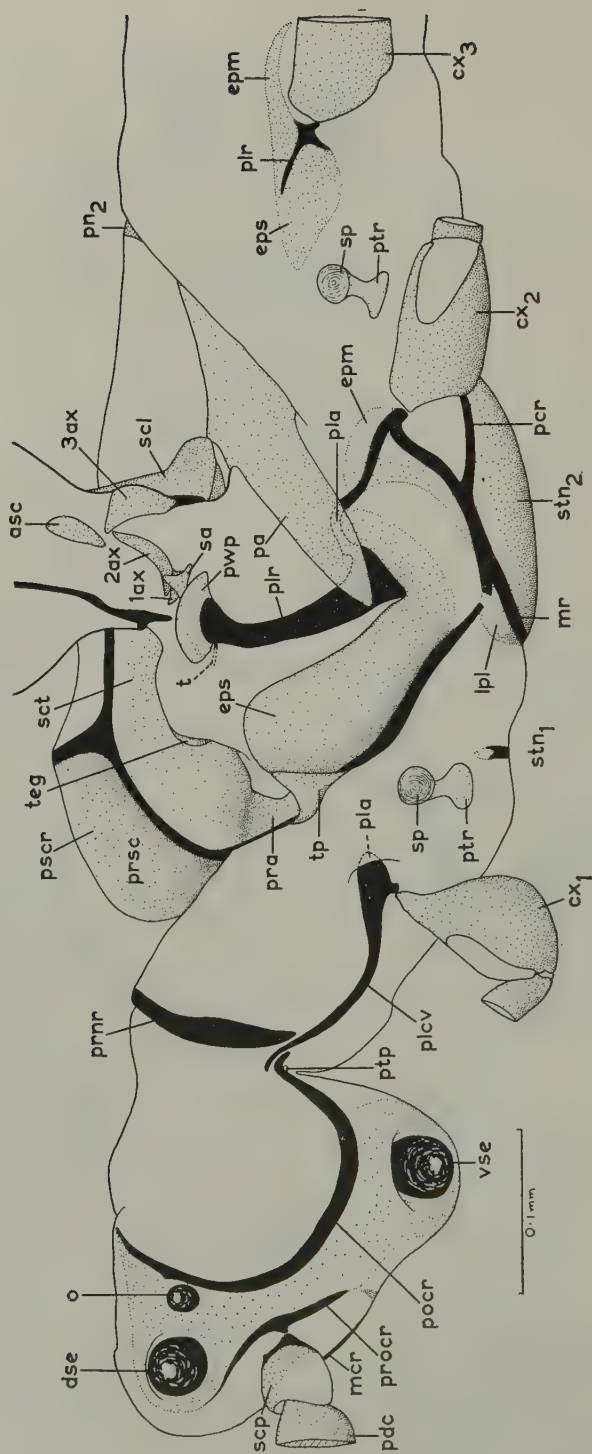
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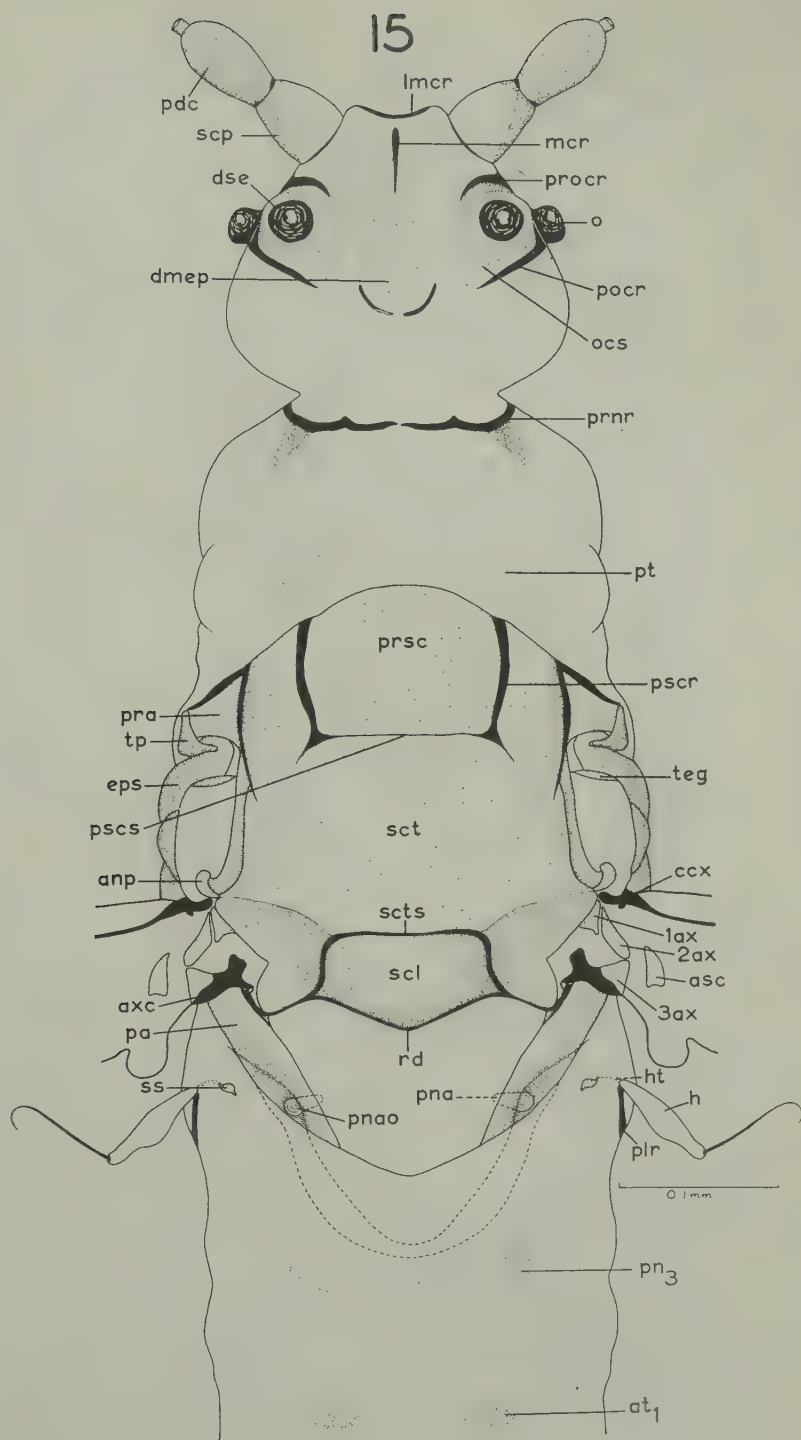


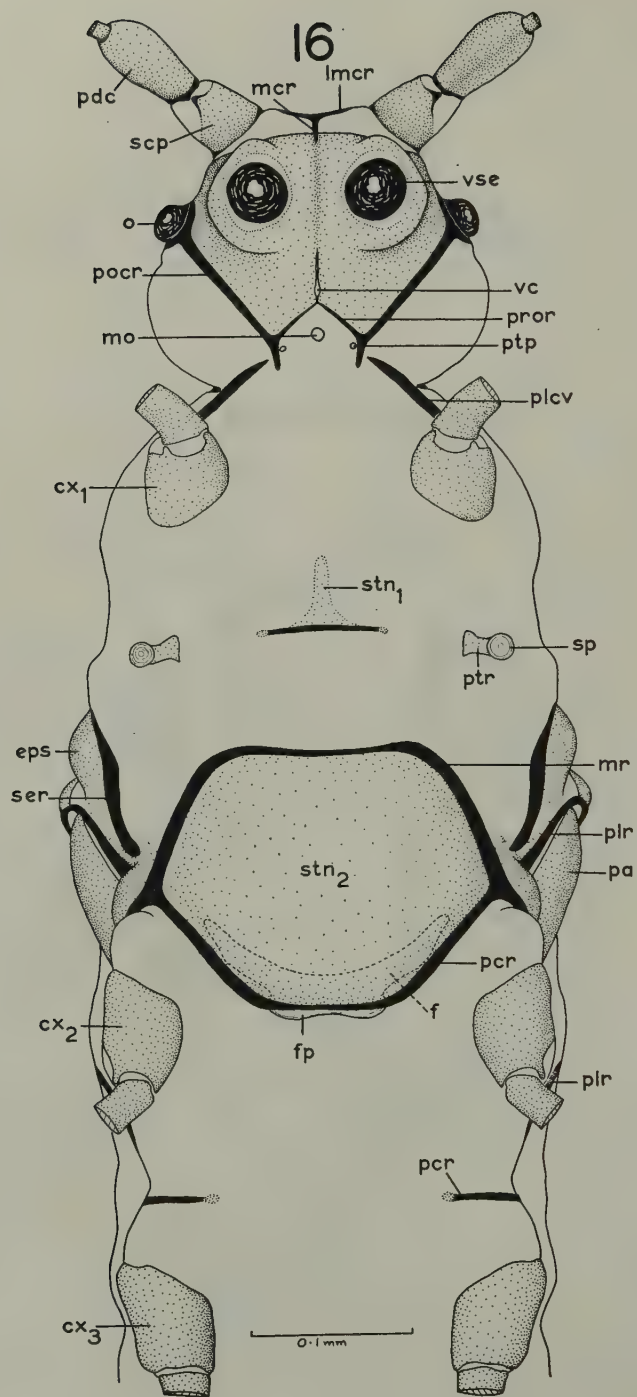


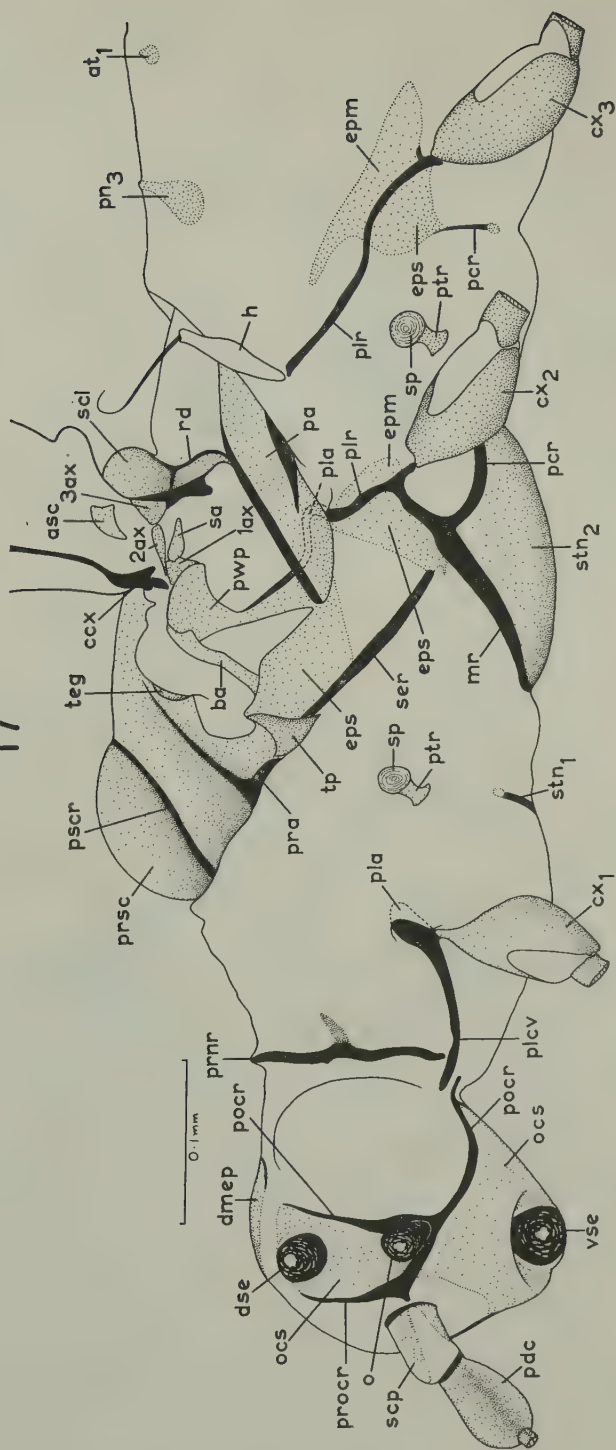


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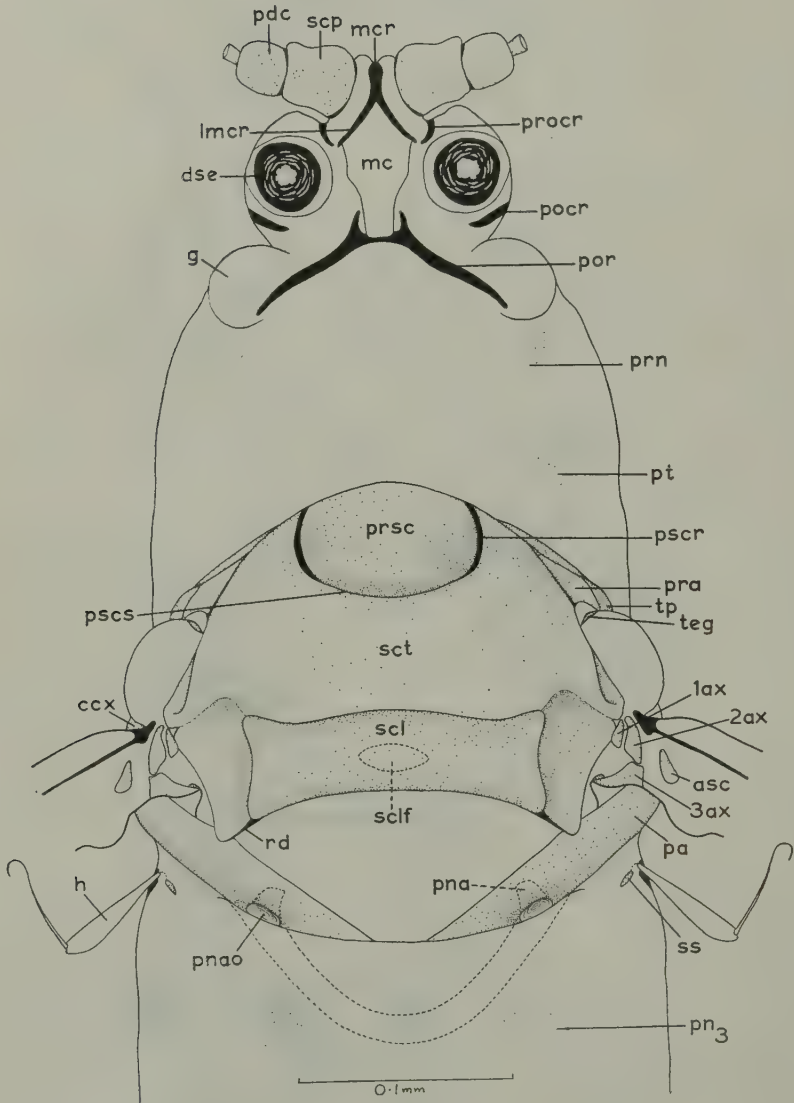




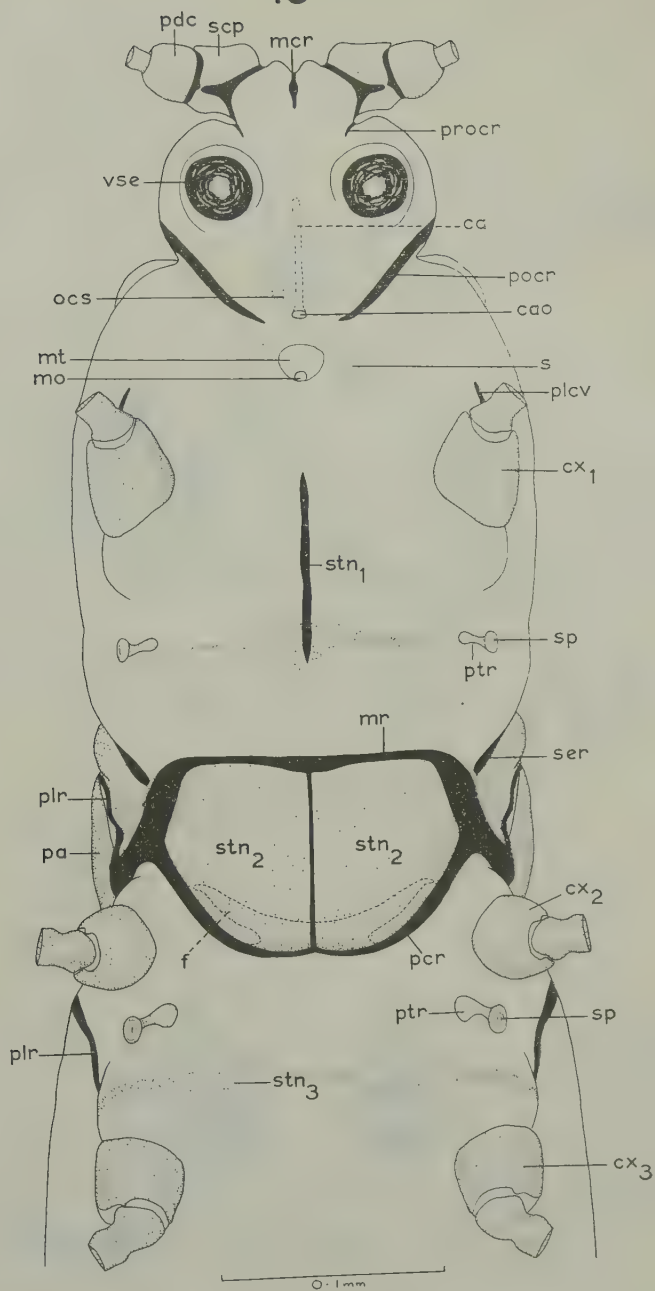


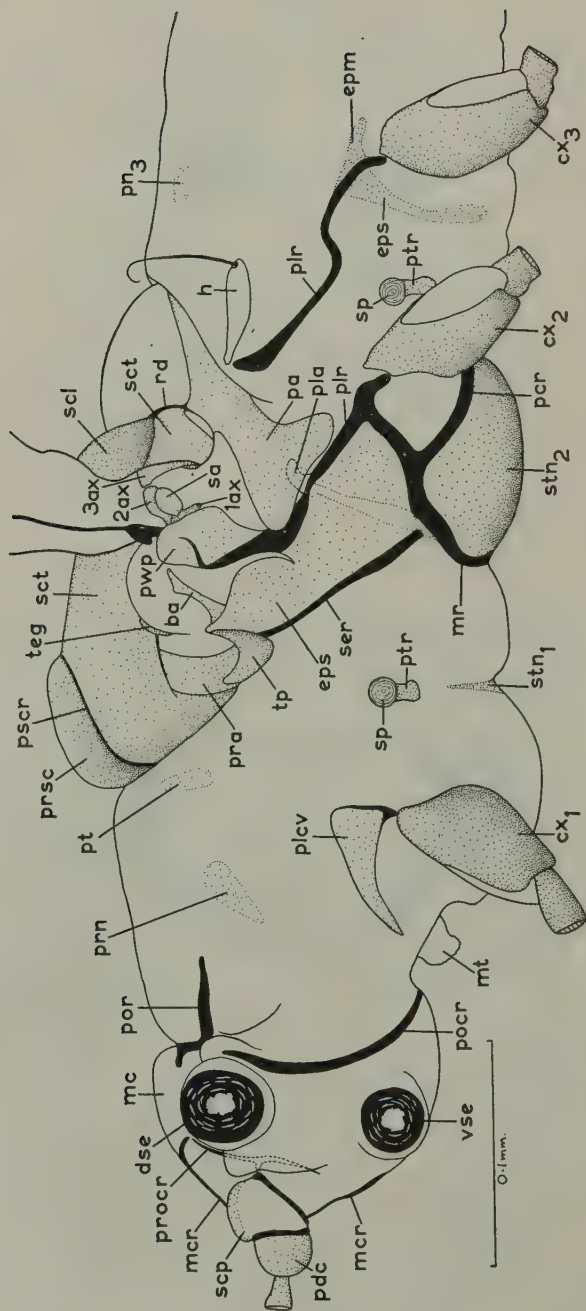


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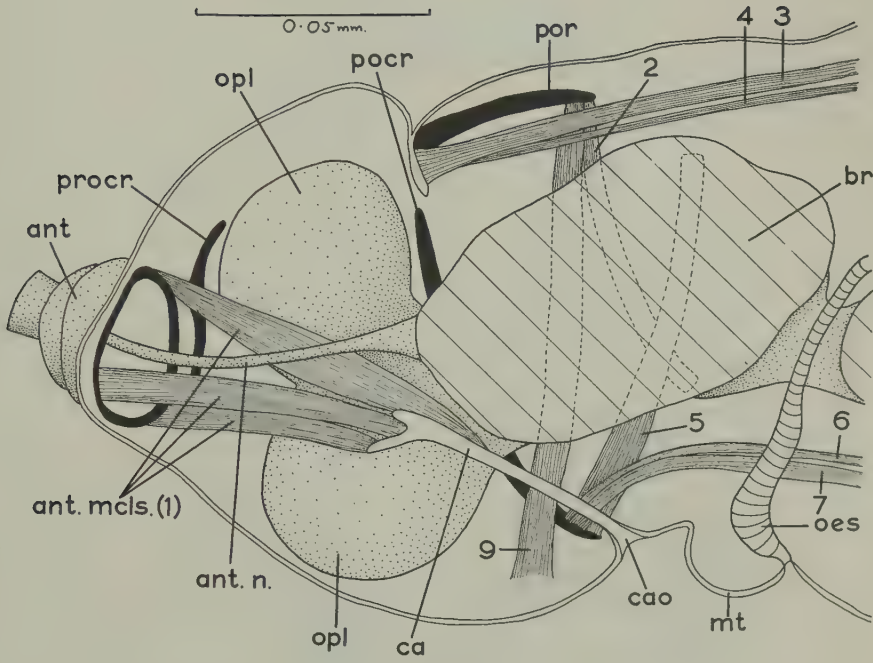


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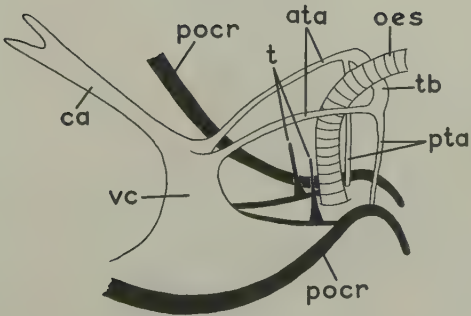




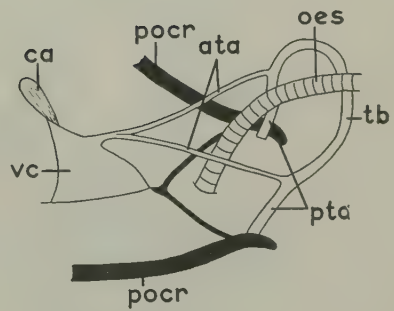
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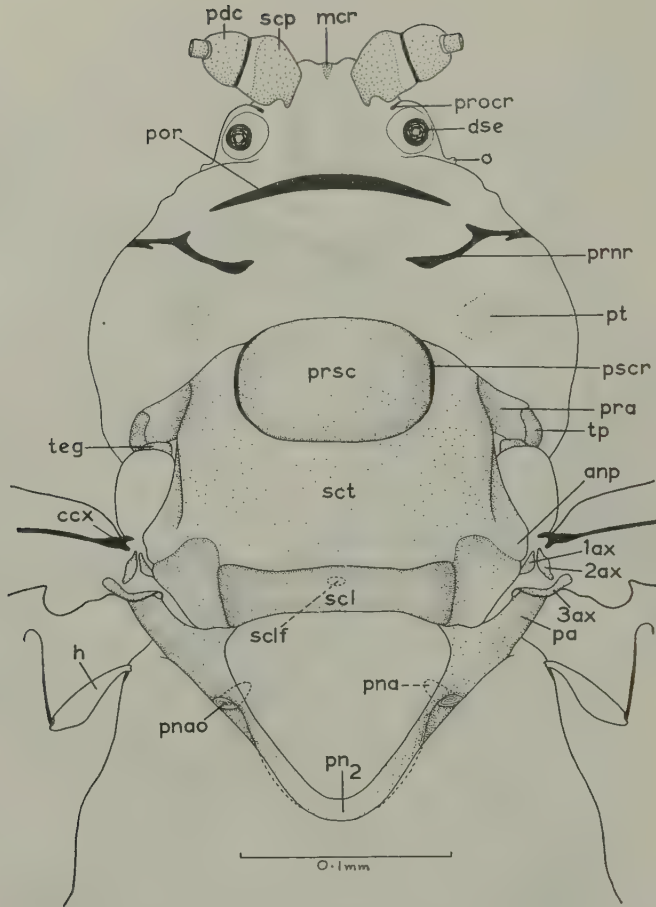
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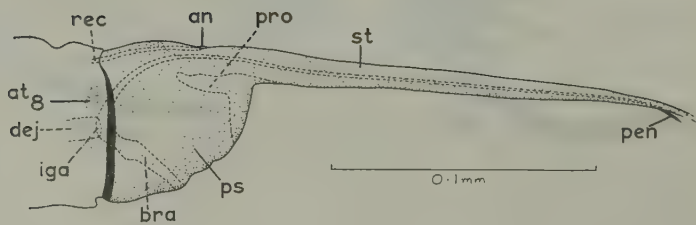
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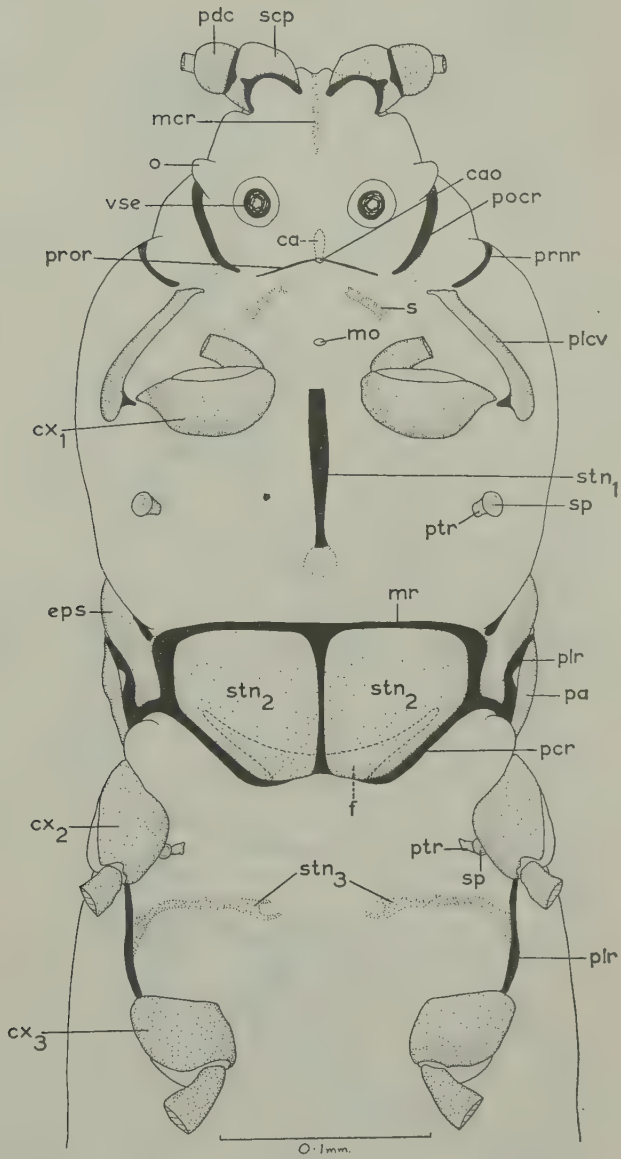
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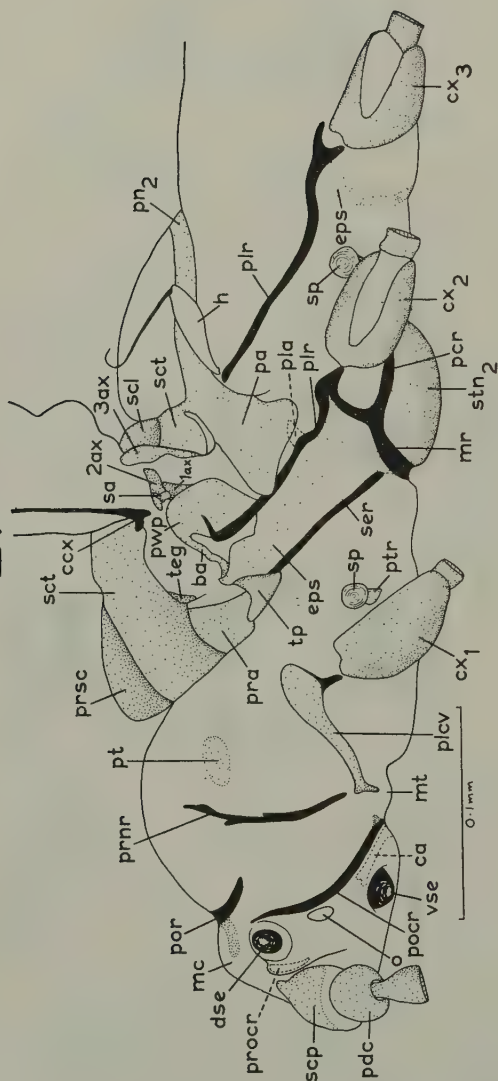
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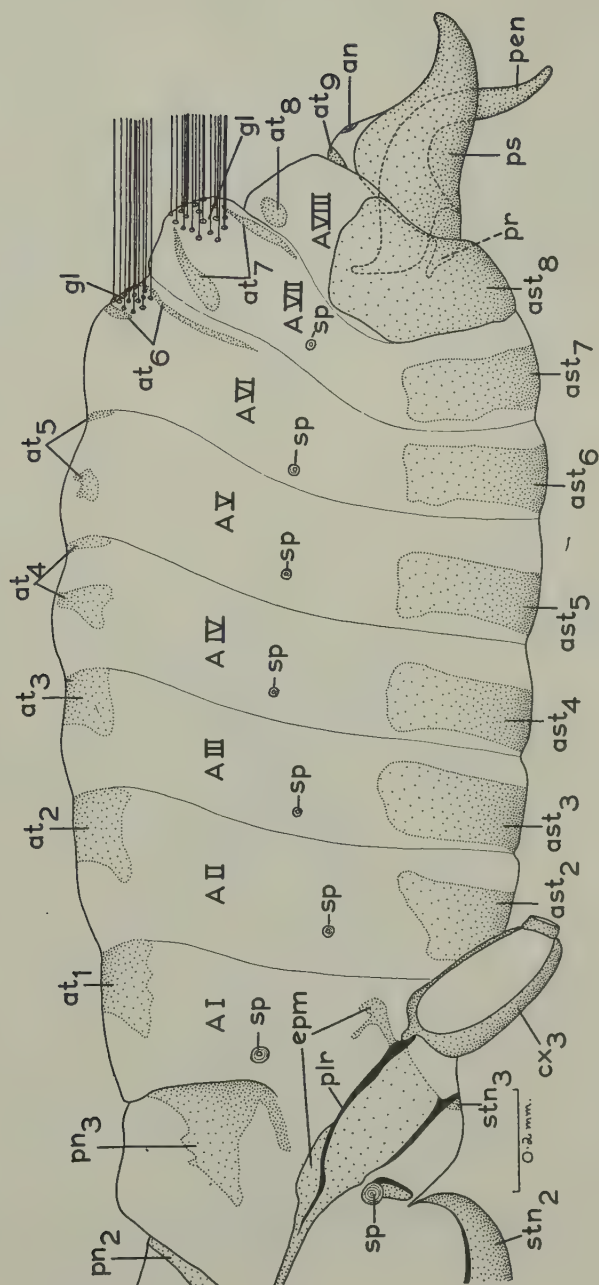


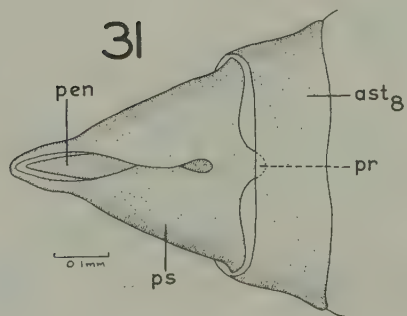
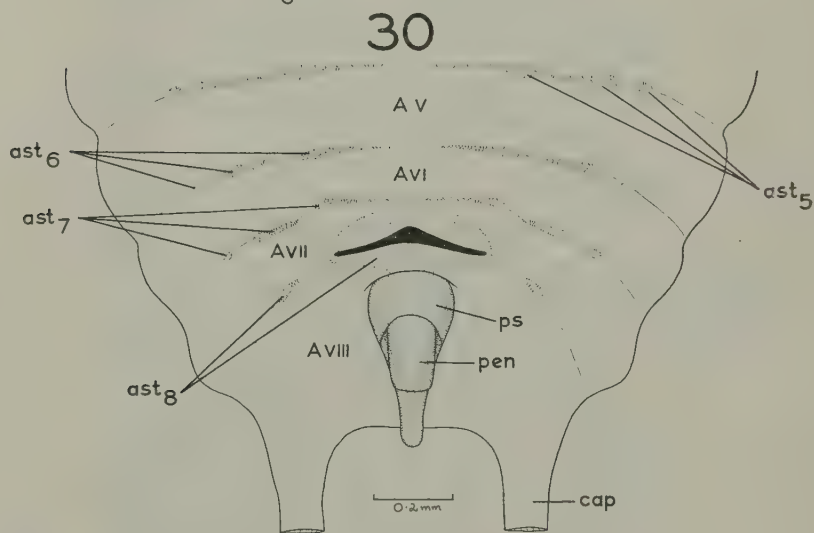
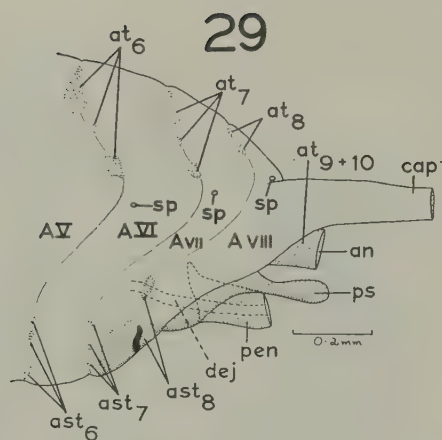
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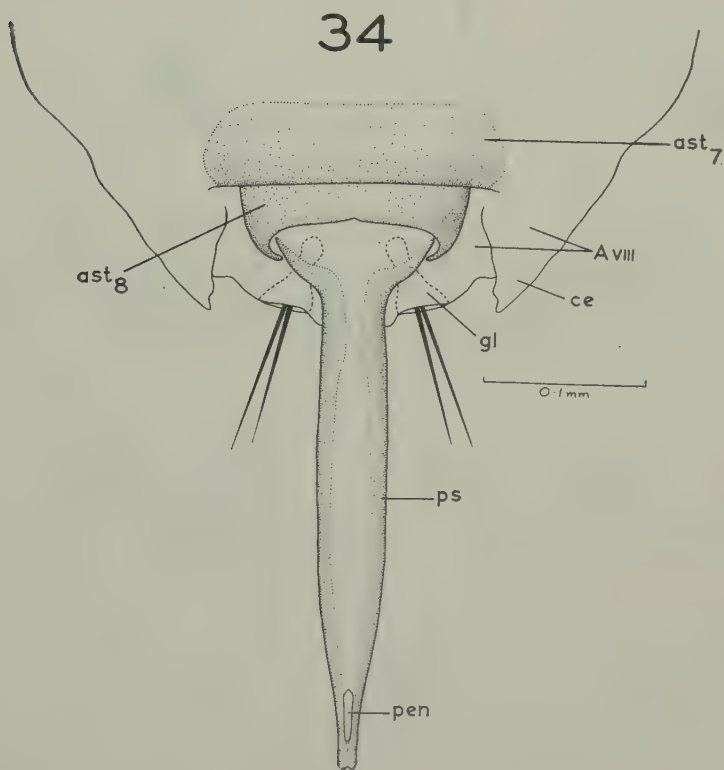
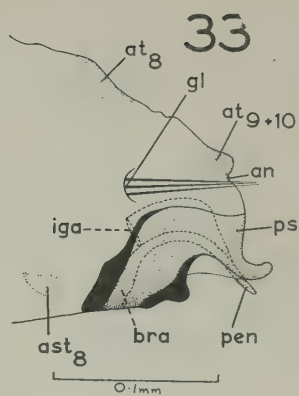
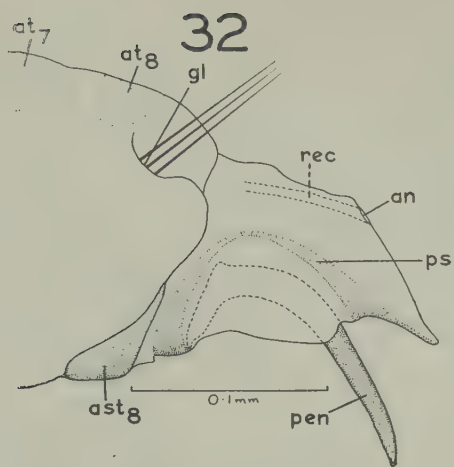


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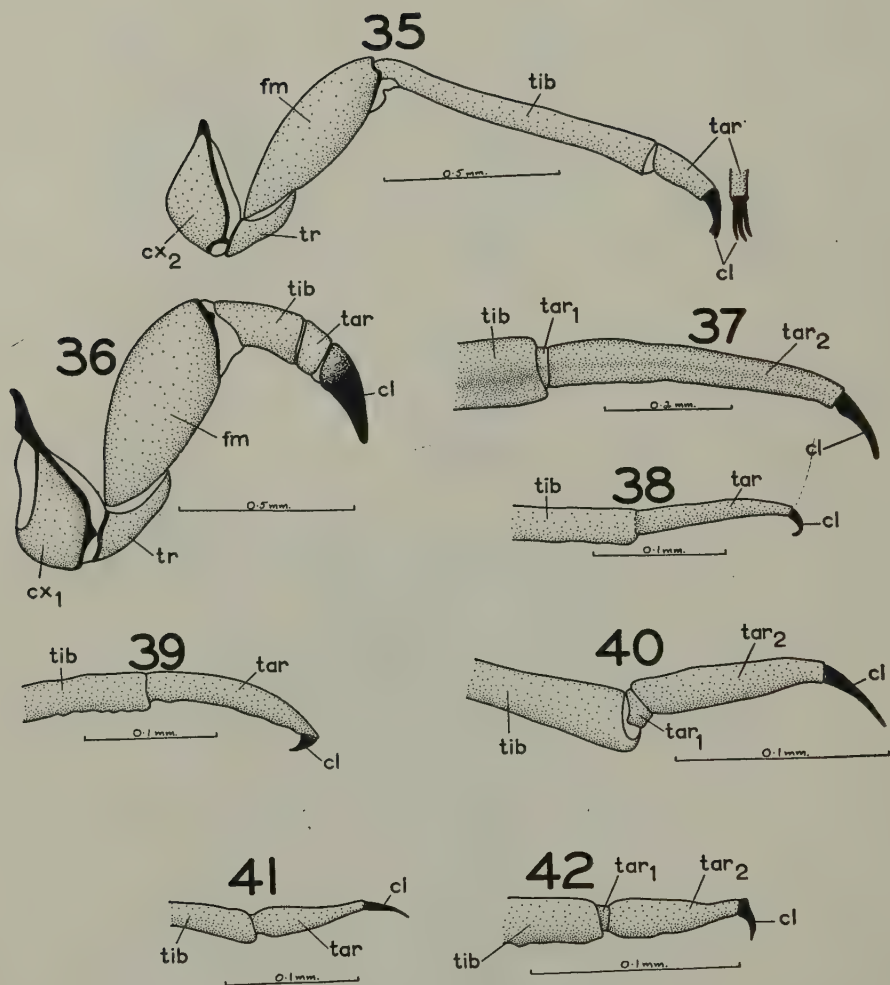




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